Limnobiology of Cowichan Lake, British Columbia

By G. Clifford Carl[1]
Pacific Biological Station, Nanaimo, B.C.
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ABSTRACT

Cowichan Lake is 34 kilometres long, up to 4 kilometres wide and up to 150 metres deep, with an area of 62 square kilometres. Its average depth is 51 metres. Its shores are of precipitous rock for over half their length, the remainder being boulders or gravel, with a very little marsh.

Summer surface temperatures are usually close to 20°C., while the winter minimum in 1938 was 5.0°. Oxygen is generally abundant in the lake, the lowest value observed being 3.4 cc. per litre, just before the fall overturn (November 24, 1939). The reaction of the water is alkaline (pH 7.0–7.8), and its bicarbonate content was 18-22 mg. per litre (as $CaCO_3$).

Lists are presented of organisms collected in the lake. The plankton is reasonably rich in variety but was poor in quantity, in 1940 at least. Bottom organisms also are not abundant. Two species of lampreys and three fishes were found in the lake, plus a number of Salmonidae whose occurrence is described elsewhere.

INTRODUCTION

The objectives and history of the investigations carried on by the Fisheries Research Board on the Cowichan River system have been set forth by Neave (1949) in his account of the salmon and trout populations. The present account describes the more general hydrographical, chemical and biological features of the watershed, especially Cowichan Lake. Though incomplete, the material presented adds to the general limnological knowledge and may form a basis for possible further work in the Cowichan system.

The material upon which the present contribution is based was gathered in 1934 and 1935, when preliminary work was done, and during the period June 1937 to September 1940 when year-round observations were made.

PHYSIOGRAPHY AND HYDROGRAPHY

Location and Origin

Cowichan Lake (Figure 1) is located in the central portion of Vancouver Island, British Columbia, at a point about midway between the east and west coasts of the island. Its geographic position may be given as Latitude 48° 50′ North and Longitude 124° 15′ West. The lake is 533 feet above sea level.

The Cowichan Valley which is occupied by the lake, river and bay is of a type known geologically as "subsequent" since its general direction conforms to the strike of the underlying rocks (Clapp, 1912). The valley has been developed by the more rapid erosion of the weaker formations of Tertiary origin while subsequent glaciation has deepened the upper end, forming the lake basin and

[1]Present address: Provincial Museum, Victoria, B.C.

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flattening the valley floor between the lake and the sea. A geologically recent uplift caused the river to entrench itself in its own flood plain with the result that in the middle part of its course, the river is confined by rock walls and has a steep grade with a few falls. The largest of these is Skutz Falls with a total drop of 18 feet in a run of 300 feet.

Near the lake there are one or two outcroppings of crystalline limestone, the most conspicuous of these being near the base of Bald Mountain; hence the name Marble Bay for the inlet near the outcropping. A fossiliferous area, possibly of Cretaceous origin, is present on the south shore of the main lake about opposite the mill town of Youbou.

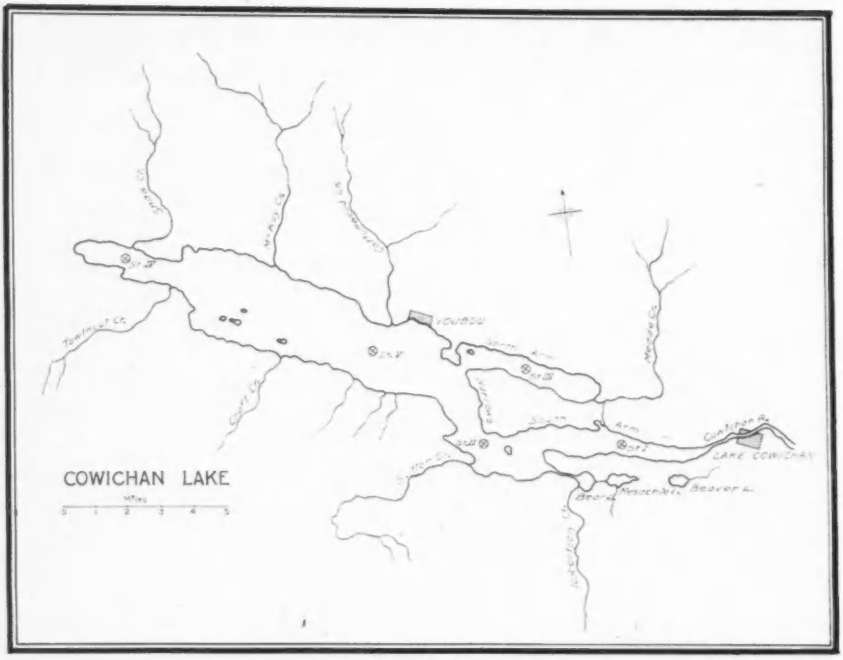

FIGURE 1. Cowichan Lake.

CLIMATE

The climate of the Cowichan Lake area is mild and moist, characteristic of the coastal region of the Province. Air temperatures during the summer seldom exceed 80° Fahrenheit, although on occasion they reach 100° in the shade. In winter, freezing weather is sometimes experienced when the temperature may drop to a few degrees above zero Fahrenheit for short periods. Ice has been known to cover only portions of the surface of the lake and this occurrence is said to be rare. The average monthly temperature for the year is 49° Fahrenheit.

The precipitation recorded at the Cowichan Lake Fish Hatchery has varied between 63.33 inches in 1938 and 90.55 inches in 1937 (161–230 cm.); part of this is contributed by snow, which averaged 34.5 inches (88 cm.) in depth over a ten-year period (Climate of British Columbia, 1937). The monthly distribution of precipitation for the period 1937 to 1941 inclusive is shown in Table I.

TABLE I. Monthly distribution of precipitation in inches at Cowichan Lake Hatchery, 1937 to 1941. (Snowfall included in precipitation.)

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Total	Year
Precipitation	3.33	13.66	3.46	13.03	4.31	6.39	T	2.49	3.14	7.96	13.26	19.52	90.55	1937
Snowfall	26.3	50.0	..	..	..	..	..	..	..	..	1.7	38.2	116.2	1937
Precipitation	8.12	6.18	11.25	2.49	0.93	0.65	0.40	0.37	2.29	8.88	6.38	15.41	63.35	1938
Snowfall	11.1	16.0	4.4	..	..	..	..	..	..	..	..	3.5	35.0	1938
Precipitation	14.64	6.95	3.48	4.61	3.24	1.64	1.84	0.33	1.27	6.91	14.35	25.38	84.64	1939
Snowfall	2.7	8.6	2.2	..	..	..	..	..	..	..	..	..	13.5	1939
Precipitation	7.95	13.35	8.77	4.61	2.47	0.58	2.43	0.52	1.35	13.39	7.75	15.28	78.45	1940
Snowfall	2.8	2.5	..	..	..	..	..	..	..	..	1.5	..	6.8	1940
Precipitation	14.19	5.74	3.46	2.77	9.85	1.96	0.23	1.26	5.20	9.53	12.73	17.16	84.08	1941
Snowfall	..	2.0	..	..	..	..	..	..	..	..	..	..	2.0	1941

VEGETATION

The area around the lake and extending down the Cowichan Valley was at one time heavily forested with extensive stands of Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.), cedar (*Thuja plicata* Donn), hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.), with occasional stands of balsam fir (*Abies grandis* (Dougl.) Lindl.), lodgepole pine (*Pinus contorta* Dougl.), arbutus (*Arbutus menziesii* Pursh.), maple (*Acer macrophyllum* Pursh.), willow (*Salix* spp.), and cottonwood (*Populus trichocarpa* T. & G.). To a great extent this cover has been removed by logging and subsequent burning of slash, with the result that a great part of the watershed is denuded of large trees (Figures 2-4). In some areas, as in the experimental plots of the Forest Branch, second-growth trees of some size occur but in most of the deforested areas little reforestation has taken place.

Along creek-bottoms and in unlogged areas the undergrowth is extremely heavy, consisting of salal (*Gaultheria shallon* Pursh.), thimbleberry (*Rubus parviflorus* Nutt.), salmonberry (*Rubus spectabilis* Pursh.), ferns (*Polystichum munitum* (Kaulf.) Underw., *Athyrium filix-femina* (L.), Roth., and *Polypodium hesperium* Maxon), and devil's club (*Oplopanax horridus* (Sm.) Miq.).

DRAINAGE

Cowichan Lake is fed by eight or ten major streams which enter at widely separated points. These streams drain the surrounding highlands and are of the

FIGURE 2. Cowichan Lake, lower end, showing the village, Hatchery, and Hatchery pool (centre); Beaver Lake (lower left); Grant Lake (right). (B.C. Government Air Photograph, 1946.)

typical mountain type with long, gravelly reaches and swift, cold water. During the rainy season these tributaries are subject to flood conditions with much shifting of the gravel and boulders along the bottom and with a tendency to form bars across the mouths. During the dry season the flow of most of the streams is much reduced with the result that considerable portions of the lower reaches of some are completely dry or consist of isolated pools connected by trickles of water flowing beneath the gravel.

Following a fairly severe earthquake in June 1946, it was noted that in several instances the gravel bar off the mouth of a stream had slumped into deep water, clearing the approach to the stream mouth and inundating groups of willows and other bushes growing on the site.

FIGURE 3. Cowichan Lake, South Arm, showing Marble Bay (top centre), Forestry reserve (upper left), Bear Lake and Robertson River (left centre), Mill site (centre) and Mesachie Lake (right centre). (B.C. Government Air Photograph, 1946.)

A number of small springs enter the lake. Two along the north shore of the South Arm enter below the surface of the lake and are evident by reason of a saucer-shaped depression at the point of entry of each spring. In summer large aggregations of fingerlings are sometimes seen near these cold-water sources. A similar spring emerges from the ground a few yards above the beach near the mouth of Meade Creek on the North Arm.

The lake drains by way of the Cowichan River which leaves the eastern end of the lake and flows in an easterly direction for approximately 28 miles down the Cowichan Valley (Figure 1). It empties into Cowichan Bay which opens into Georgia Strait.

The area drained by this lake and river system is about 235 square miles (609

FIGURE 4. Cowichan Lake, north shore, showing effect of intensive logging activities in Shaw Creek valley. (B.C. Government Air Photograph, 1946.)

sq. km.). The greater part of the watershed consists of mountain slopes while the smaller part, situated at the mouths of the tributary valleys and along the river, is more or less flat. A small part is under cultivation.

A conspicuous feature of the watershed is the evidence of the extensive logging operations that have been carried on for over thirty years. Practically the whole lake is now girdled with a deforested belt (Figures 2-4) extending from lake level (533 feet) to an altitude of 1500 feet (163–460 m.). The narrow belt on either side of the river has also been "logged-off" and burnt over, and new growth is scant in this area.

Run-off data for the river are available for the years 1913 to 1919 inclusive and from September 1940 to the present time. These show that the time of greatest run-off occurs in the winter months (November to January) and that the

time of least run-off occurs in August and September. Details are presented by Neave (1949).

The relation between precipitation and run-off is of some considerable interest since the biological conditions in the river, including the mass movements of fishes, are greatly affected by the volume of flow. From data available it may be seen that the amount of run-off follows very closely the amount of precipitation as recorded at the hatchery, the former lagging slightly behind the latter in terms of time. Since the amount of precipitation in the form of snow was small in 1941 (2.0 inches at lake level) this relationship seems to indicate that there is little storage of ground water on the watershed.

Size and Shoreline

The lake is approximately 21 miles long and 0.25 to about 2.5 wide (34 by 0.4-4 km.), with an area of 23.8 square miles (62 sq. km.). In general, the lake is narrow; it consists of a larger portion and two smaller portions locally called the North Arm and the South Arm. A short section called the Narrows connects the South Arm with the main lake (Figure 1). Near the outlet there are three small shallow lakes. First in importance is Mesachie Lake (188 acres or 76 hectares in area) which drains into Bear Lake (area 68 acres, 28 hectares) which in turn is connected to Cowichan Lake by a short, narrow passage (Figures 3, 5). East of Mesachie Lake is Beaver Lake (80 acres, 33 hectares) which flows into Cowichan River by way of a small winding stream (Figure 2).

The shoreline is quite irregular and is fairly long (64 miles, 103 km.) in proportion to the area of the lake. By dividing the length of the shoreline of a lake by the length of the circumference of a circle of the same area a figure is obtained which has sometimes been used as an index of productivity. This is based on the assumption that near-shore areas are usually the most productive. In the case of Cowichan Lake the figure so obtained is 3.70. Comparisons with certain other lakes in the Province can be made as follows:

Cultus Lake 1.53 (Ricker, 1937);

Okanagan Lake 3.9 (Clemens, Rawson and McHugh, 1939);

Paul Lake 5.55 (Rawson, 1934).

This method of indicating productivity is misleading, however, in the case of Cowichan Lake, since a large part of the shore consists of precipitous rocky slopes which fall rapidly away into deep water. The remaining portion of the shore shows less abrupt but yet quite steep slopes, with the result that little of the near-shore area overlies productive shallows.

The shore may roughly be divided into four main types as follows:

Precipitous rock	55 per cent;
Gravel	35 per cent;
Boulders	3 per cent;
Marsh	2 per cent;

A shore consisting of such a large proportion of rocky material bordering deep water provides little anchorage for plants and little shelter for aquatic animals. In only a few of the more sheltered coves the shore and bottom consist of soft mud or ooze supporting an abundant plant growth.

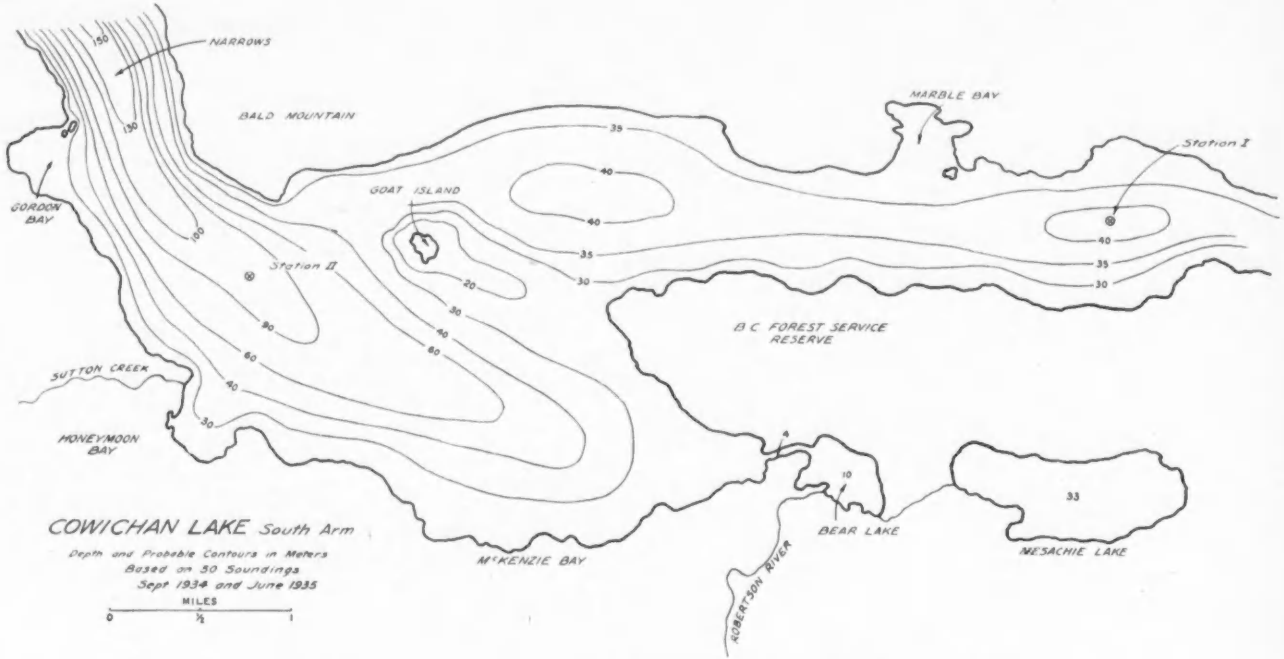

FIGURE 5. Cowichan Lake, South Arm, showing depths and probable contours in metres.

Depth and Volume

In general, Cowichan Lake is deep, the maximum depth measured being 150 metres (492 feet) between Youbou and the Narrows. In the course of the investigation about 200 soundings were made in various parts of the lake and from these records were constructed the approximate depth contours shown in Figures 5 and 6. From these contours it may be seen that the deepest area, 150 metres, lies at the entrance to the Narrows and is rather small in extent. The Narrows appears to have been formed by a fault which extends well into the South Arm of the lake. The North Arm is 89 metres deep (292 feet) and is partially separated from the remaining portion of the lake by a bar across the mouth where the water is only 42 metres deep (138 feet). A maximum depth of 40 metres is attained in the South Arm at two points and a fairly extensive shallow area (2 to 10 metres in depth) exists south and east of Goat Island.

The areas included within the contours shown on the map were obtained by the use of a planimeter and are given in Table II. From this it will be seen that a relatively small portion (14.8 per cent) of the lake area is less than 10 metres (33 feet) deep while 73 per cent of the total area lies over water more than 20 metres (66 feet) deep and 46 per cent lies over water more than 50 metres (164 feet) deep.

The approximate volume of water within each contour interval has been calculated by multiplying the area by the average depth. These data, expressed in acre-feet and in millions of cubic metres, are included in Table II which also gives the per cent of the total volume. It may be noted that the 10-metre interval comprising the greatest volume (14.5 per cent of the total) is the 80- to 90-metre zone while the volume of water overlying the greatest depth zone is very small. Over 50 per cent of the total volume of the lake lies over depths greater than 80 metres (262 feet).

Table II. Area and volume data for Cowichan Lake.

Contour interval	Area		Percentage of total area	Volume		Percentage of total volume
m.	*acres*	*hectares*		*acre-feet*	$m.^3/10^6$	
0– 10	2,287	925.5	14.8	37,500	46.3	1.4
10– 20	1,848	747.7	12.1	90,900	112.2	3.5
20– 30	1,392	563.4	9.1	114,100	140.8	4.4
30– 40	1,656	670.2	10.8	190,100	234.6	7.4
40– 50	1,228	496.8	8.0	181,300	223.6	7.0
50– 60	1,124	454.8	7.3	202,800	250.1	7.9
60– 70	1,024	414.4	6.7	218,300	269.4	8.5
70– 80	884	357.6	5.8	217,500	268.2	8.4
80– 90	1,296	524.4	8.5	361,300	445.7	14.5
90–100	748	302.6	4.8	233,800	287.5	9.6
100–125	1,080	437.8	7.7	396,400	490.3	15.4
125–150	556	225.0	3.6	249,800	318.2	10.3
150–	140	56.7	0.8	68,900	85.0	1.7
Total	15,263	6176.9	100.0	2,349,883	3,171.956	100.0

Bottom Deposits

The bottom deposit of a large part of the near-shore area consists of gravel and coarse sand except in those parts flanking steep, rocky shores which fall abruptly into deep water. A few areas of fine sand or soft mud occur in the shallow waters but for the most part the bottom cover in this zone is of a stony nature. In deeper water, ranging from 4 metres (13 feet) in some places to the deepest parts, soft mud or ooze predominates. In the vicinity of booming grounds this is often overlaid with a covering of small bits of bark and other debris resulting from logging operations. A few areas of sand, gravel or clay were encountered in water up to 30 metres (108 feet) in depth in various parts of the lake.

PHYSICAL AND CHEMICAL CONDITIONS

Apparatus and Methods

Observations on the lake were carried out from a 26-foot cabin launch. All temperature readings, both at the various stations on the lake and at the boathouse on the river, were taken by means of a Negretti and Zambra deep-sea reversing thermometer graduated to fifths of a degree Centigrade. Readings were made to the nearest tenth of a degree and no correction was made for possible expansion due to changes in water pressure.

Water samples were taken at the same time as the temperature observations by means of a Kemmerer water bottle. Determinations of dissolved oxygen content were made by the Winkler method. During 1937 and 1938 the thiosulphate solution used in the titrations was standardized against potassium bichromate of known strength, but during 1939 and 1940 the solution was standardized by the use of a well-shaken sample of lake water which was assumed to be 100 per cent saturated with dissolved oxygen.

Determinations of hydrogen ion content (pH) were made by the colorimetric method, while determinations of carbonate content were made by titrating with M/50 sulphuric acid and using methyl orange as an indicator.

Plankton samples were collected by means of a "Wisconsin" type net during the major part of the investigation but for quantitative results a 10-litre Juday plankton trap was used in 1940.

As the greater part of the observations and sampling was carried out at Station I, a wooden buoy was permanently anchored at this point in October 1939 to eliminate the difficulties and errors introduced by drifting.

Bottom samples were collected by means of an Ekman dredge which covered an area of 520 square centimetres (81 square inches). The samples collected were washed through a series of fine-meshed screens from which the organisms were recovered.

Temperature

Temperature observations were made at five stations in the lake as shown in Figures 5 and 6. Station I was located in the South Arm; Station II was near the entrance to the Narrows; Station III was in the North Arm; Station IV, opposite

Shaw Creek near the upper end of the lake and Station V was in the main lake opposite Cottonwood Creek mouth.

Vertical series of temperature readings were taken at Station I during the following periods: (*a*) June, July and August of 1935 (weekly intervals); (*b*) June 1937, to December 1938 (approximately fortnightly intervals), and (*c*) January 1939 to December 1940 (monthly intervals). These records are presented in Table III. A few other vertical series were taken at Stations II to V (Table IV). In addition daily temperature readings, morning and evening, were taken of the Cowichan River two feet below the surface at the Hatchery boathouse.

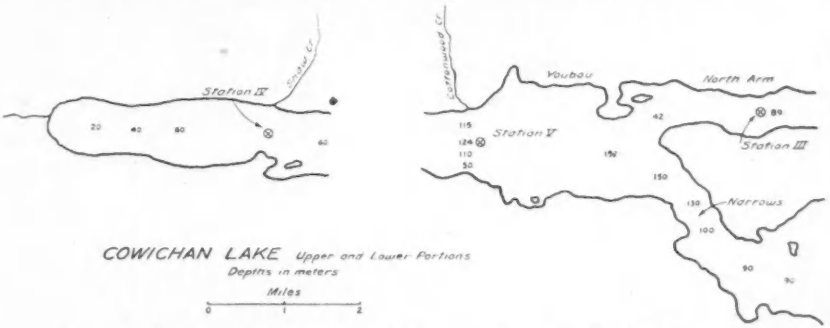

FIGURE 6. Cowichan Lake, upper and lower portions showing depths in metres.

Owing to its remoteness, it was impractical to take temperature and other records regularly in the deepest portion of the lake. For this reason vertical series were mostly taken at Station I in the South Arm which was within reasonable distance of the Hatchery. To test the applicability of these records to the lake as a whole, observations were made at Station I and at Station IV at the upper end of the main lake during the same day on two occasions, July 11, 1935, and July 26, 1939. The results of these observations are shown in Figure 7, from which it may be seen that there was considerable discrepancy, particularly on the first occasion. From these and other observations it would appear that summer temperatures for the epilimnion (upper 10 metres approximately) at Station I in the South Arm were consistently higher than those in the main lake and that these variations in thermal conditions were produced by the action of prevailing winds.

TABLE III. (A) Temperature readings for Cowichan Lake in degrees Centigrade, 1935, at Station I.

Depth (metres)	June 21	July 4	July 11	July 18	July 25	Aug 1	Aug 8	Aug 18
0	16.5	16.5	16.4	20.0	20.8	20.3	19.2	19.8
5	15.7	16.5	16.4	14.2	20.8	19.9	19.2	18.7
10	15.1	16.4	16.3	17.4	20.2	19.7	19.0	18.4
15	13.7	14.2	13.8	14.1	15.0	15.5	15.0	14.3
17.5	..	11.4	11.6	11.4	11.2	11.6	11.5	10.3
20	8.9	8.8	10.6	9.2	9.4	8.9	9.2	9.3
35	..	6.7	6.8	6.8	6.9	6.9	7.0	7.1

TABLE III. (B) Temperature readings for Cowichan Lake in degrees Centigrade, 1937, at Station I.

Depth (metres)	June 8	June 17	June 24	July 1	July 8	July 16	July 23	July 29	Aug 5	Aug 12	Aug 20	Aug 29	Sept 5	Sept 12	Sept 19	Sept 30	Oct 7	Oct 17	Oct 28	Nov 6	Nov 14	Nov 26	Dec 7	Dec 21
0	16.4	15.1	15.6	17.5	18.4	19.3	20.4	20.8	20.2	20.2	19.4	18.5	18.3	18.9	18.2	16.0	15.2	14.9	14.2	12.5	10.7	9.1	8.4	7.6
5	15.5	13.6	14.1	16.7	18.0	19.0	19.7	20.8	20.2	19.9	14.3	18.2	18.2	18.4	18.2	16.0	15.1	14.7	14.2	12.5	10.7	..	..	..
7.5	..	11.7	14.0	15.6	17.0	18.1	19.2	20.8	19.9	19.6	19.3	..	..	..	..	..	15.0	..	..	..	..	..	..	..
10	14.6	10.9	13.3	14.3	16.6	17.6	..	20.7	19.8	19.2	19.2	18.0	18.3	18.2	18.2	11.5	15.0	14.7	14.1	12.5	..	..	..	..
12.5	..	..	..	..	14.8	15.1	12.8	18.2	18.0	16.9	16.9	..	18.2	17.8	17.7	10.3	15.0	14.6	13.8	12.5	10.7	..	..	..
15	13.4	9.0	10.2	9.1	10.6	10.8	11.8	17.2	16.0	15.9	16.6	13.4	15.4	16.4	14.4	9.9	14.9	14.6	13.8	12.5	10.7	..	..	..
17.5	10.0	8.3	9.3	9.0	8.8	8.95	8.6	11.7	9.7	9.3	10.1	9.7	11.1	13.7	10.2	9.0	12.8	14.6	11.9	11.2	10.6	9.1	..	..
20	7.7	7.7	8.1	8.5	8.4	8.6	8.4	9.9	9.4	9.2	9.5	8.5	9.4	9.3	8.9	8.8	10.0	11.3	10.8	11.1	10.4	9.1	..	..
25	..	..	..	..	..	..	..	..	..	8.0	..	..	8.2	8.2	7.9	8.4	8.5	8.6	8.9	8.6	8.8	9.1	8.55	7.6
35	6.6	6.6	6.9	6.8	7.0	7.0	7.0	7.1	7.1	7.1	7.2	7.4	7.5	7.6	7.4	7.6	7.6	7.5	8.0	7.7	7.8	8.0	8.1	7.5

TABLE III. (C) Temperature readings for Cowichan Lake in degrees Centigrade, 1938, at Station I.

Depth (metres)	Jan 5	Feb 14	Mar 3	Mar 22	Apr 10	Apr 20	May 15	May 29	June 19	July 3	July 24	Aug 1	Aug 25	Sept 11	Oct 5	Oct 20	Nov 1	Nov 30	Dec 11
0	6.4	5.0	6.0	5.5	7.6	7.9	11.9	15.7	18.5	18.8	21.6	19.6	19.5	19.6	17.7	15.2	13.5	9.0	8.0
5	..	..	5.9	..	7.0	7.9	11.1	15.7	16.6	18.5	20.8	19.6	19.3	19.1	17.1	15.2	13.3	9.0	8.0
10	..	..	5.5	..	6.8	7.6	9.9	15.7	16.2	17.5	18.9	19.5	18.7	18.8	17.1	14.9	13.3	9.0	8.0
12.5	..	..	..	..	..	..	..	..	15.6	15.2	16.6	..	..	..	..	..	..	..	..
15	..	..	5.2	5.5	6.6	7.6	9.0	12.2	11.7	11.8	15.2	18.1	17.0	17.0	17.0	14.9	11.8	8.95	8.0
17.5	..	..	..	..	..	..	..	..	..	..	12.4	15.2	15.1	14.8	16.3	14.9	..	..	..
20	..	..	..	..	..	..	7.0	8.4	8.3	7.9	11.0	10.3	10.8	9.8	11.3	12.8	9.7	9.0	8.0
25	..	..	5.1	..	5.8	5.9	6.8	7.0	7.3	7.6	8.2	8.3	8.4	8.6	8.5	8.8	8.6	8.7	8.0
35	6.2	4.9	4.95	5.5	5.5	5.6	6.1	6.4	6.5	6.9	7.0	7.4	7.6	7.8	7.4	7.6	7.8	7.8	8.0

TABLE III. (D) Temperature readings for Cowichan Lake in degrees Centigrade, 1939 and 1940, at Station I.

Depth (metres)	1939 Jan 17	Feb 20	Mar 27	May 17	July 8	July 26	Aug 15	Sept 16	Oct 11	Nov 1	Nov 24	Dec 8	1940 Jan 31	Feb 29	Mar 25	Apr 26	May 17	June 14	July 22	Sept 11	Oct 14	Dec 11
0	6.5	5.9	8.9	13.6	18.4	21.0	21.0	18.1	15.9	13.2	10.6	8.4	6.7	6.5	8.1	11.5	13.9	17.9	21.4	20.2	16.5	8.6
5	6.6	5.5	7.0	13.5	16.8	18.5	21.0	18.5	15.9	13.2	10.5	8.4	6.6	6.4	8.0	11.2	12.7	17.1	20.8	19.9	16.4	8.6
10	6.5	5.59	6.9	12.9	15.7	16.5	20.6	17.8	15.8	13.1	10.4	8.4	6.5	6.4	7.5	10.8	11.5	16.8	19.8	19.7	13.8	8.6
12.5	..	..	..	..	13.6	..	..	..	..	..	..	..	..	..	..	..	..	15.8	18.7	..	..	..
15	6.45	5.5	6.8	10.3	11.6	13.2	17.9	17.2	15.8	12.7	10.4	8.4	..	..	..	10.0	9.4	12.8	16.5	18.2	13.8	8.6
17.5	..	..	..	..	..	..	12.8	..	..	..	..	..	..	..	..	..	..	..	12.0	15.5	..	..
20	6.5	5.5	5.8	8.7	8.4	10.3	10.5	11.2	11.3	11.2	9.8	8.4	6.3	6.4	6.7	7.5	8.3	9.6	9.9	11.2	10.7	8.6
25	..	5.4	5.6	7.0	7.8	8.3	8.8	9.3	8.7	9.1	8.1	8.4	..	6.3	..	..	7.8	8.3	8.7	9.4	9.2	8.6
30	..	..	..	..	..	..	..	..	..	8.0	..	8.4	6.3	..	6.6	7.0	..	..	8.2	8.6	8.4	8.6
35	6.4	5.4	5.6	6.5	7.2	7.2	7.3	7.6	7.5	7.5	7.7	8.4	6.25	6.3	6.6	7.0	7.2	7.6	7.8	8.1	8.1	8.6

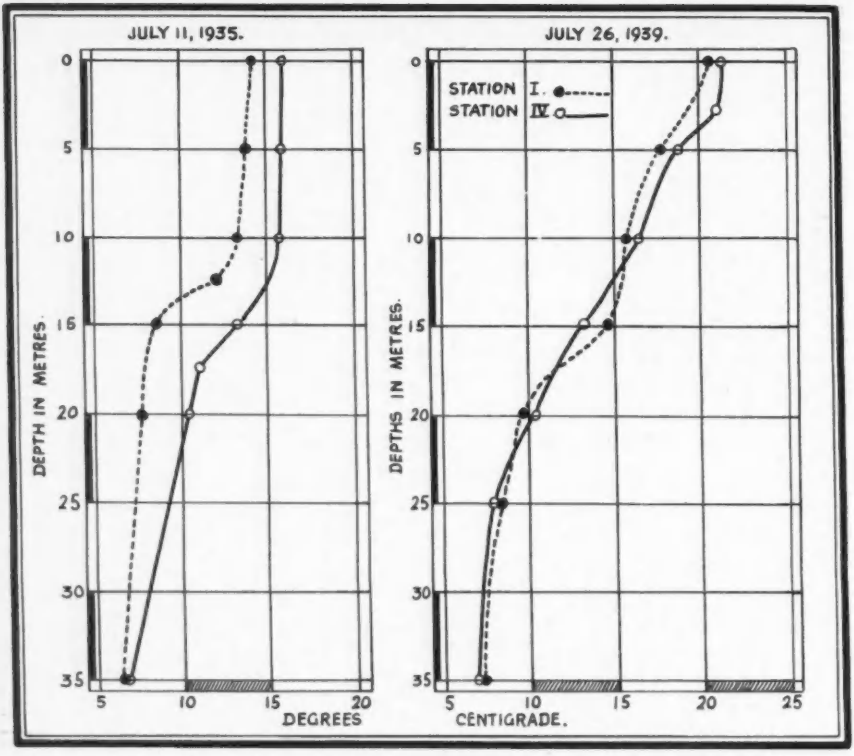

FIGURE 7. Thermal conditions at Stations I and IV, Cowichan Lake, on July 11, 1935 and July 26, 1939.

SEASONAL VARIATION

In order to show graphically the temperature changes according to the seasons the readings given in Table III are presented in the form of isotherms in Figures 8 (*a*), (*b*) and (*c*). The depth distribution of layers of water of the same temperature is thus displayed throughout the months of three consecutive years. Since Cowichan Lake rarely freezes over there are only two primary temperature seasons, winter circulation and summer stagnation.

In the late fall, when the temperature of the lake is the same from top to bottom, complete circulation is established. The exact date when this takes place apparently varies only a few days from year to year depending upon the amount of heat stored in the lake, the rapidity of cooling of the water and the presence or absence of heavy wind. In 1937 complete circulation in the South Arm became established shortly after December 7; in 1938, on December 4; in 1939, on or shortly before December 8; and in 1940, before December 11. At this time the water temperature may be from 7 to 9 degrees Centigrade. After complete circulation commences the lake continues to cool down gradually to a minimum of

about 5.5°C. During the investigational period no temperature readings below 4.9°C. were obtained in the South Arm; it is probable that temperatures lower than 4.9° existed in the main lake, but this was not ascertained. After the winter minimum is attained the upper strata of the lake begin to warm up. At this season circulation is only partial unless disturbed by violent wind action as on March 22, 1938, when the water of the South Arm was again uniformly mixed.

With the advance of the season the lake water continues to become warmed, but the rate of warming in the upper layers is so much greater than in the deeper water that stratification soon develops and circulation takes place in the upper layers only. By the end of May a "thermocline" is established, usually between the 10- and 15-metre levels. A thermocline is said to exist when a vertical temperature gradient of 1°C. or more per metre is found. Occasionally differences of as much as 5°C. have been observed in 2.5 metres as on October 5, 1938 (Table IIIc). As the summer progresses the layers of water above the thermocline ("epilimnion") continue to increase in temperature, the thermocline moves gradually downward and at the same time becomes greater in vertical extent.

Following the period of maximum water temperatures which are usually attained in July, August and September, the epilimnion begins to cool down but remains stratified until mixed by wind action in the late fall.

TABLE IV. Temperature readings for Cowichan Lake, in degrees Centigrade.

	Station II			Station III		Station IV			Station V
Depth (metres)	Sept 11 1934	June 24 1937	Aug 25 1938	June 27 1935	Aug 16 1935	July 11 1935	Aug 8 1935	July 26 1939	July 26 1935
0	19.4	15.7	19.7	17.2	19.6	14.6	16.2	20.3	20.2
5	..	14.0	19.2	15.8	18.9	14.2	15.6	17.8	18.8
10	19.4	13.4	18.4	15.3	18.6	13.8	15.5	16.0	17.7
12.5	..	..	..	..	..	12.4	..	..	..
15	19.4	11.6	17.5	14.3	14.6	8.8	14.7	14.9	13.6
17.5	15.5	10.2	16.2	..	..	..	11.4	..	..
20	13.0	9.9	13.3	8.3	8.1	7.9	8.8	10.0	8.6
30	7.7	..	7.4	6.6	6.8	..	..	..	..
35	..	6.8	..	..	..	6.6	6.5	7.3	..
50	6.8	6.2	6.4	5.8	..	..	..	..	6.2
60	..	..	..	..	..	..	..	6.8	..
80	5.6	..	..	5.5	5.6	..	..	..	..
110	..	..	..	..	..	..	..	..	5.6

The deeper waters of the lake undergo seasonal temperature changes to a lesser degree. After the winter period of complete circulation the layers of water below the thermocline ("hypolimnion") remain relatively undisturbed by wind action and the condition known as summer stagnation is said to exist. The temperature, however, slowly but steadily rises as may be seen by reference to Table IV and Figures 8 (*a*), (*b*) and (*c*). Readings taken at 35 metres show an increase from 4.9°C. on February 14 to 8.0°C. on December 11 in 1938, and lesser increases occurred during approximately the same period in the two following

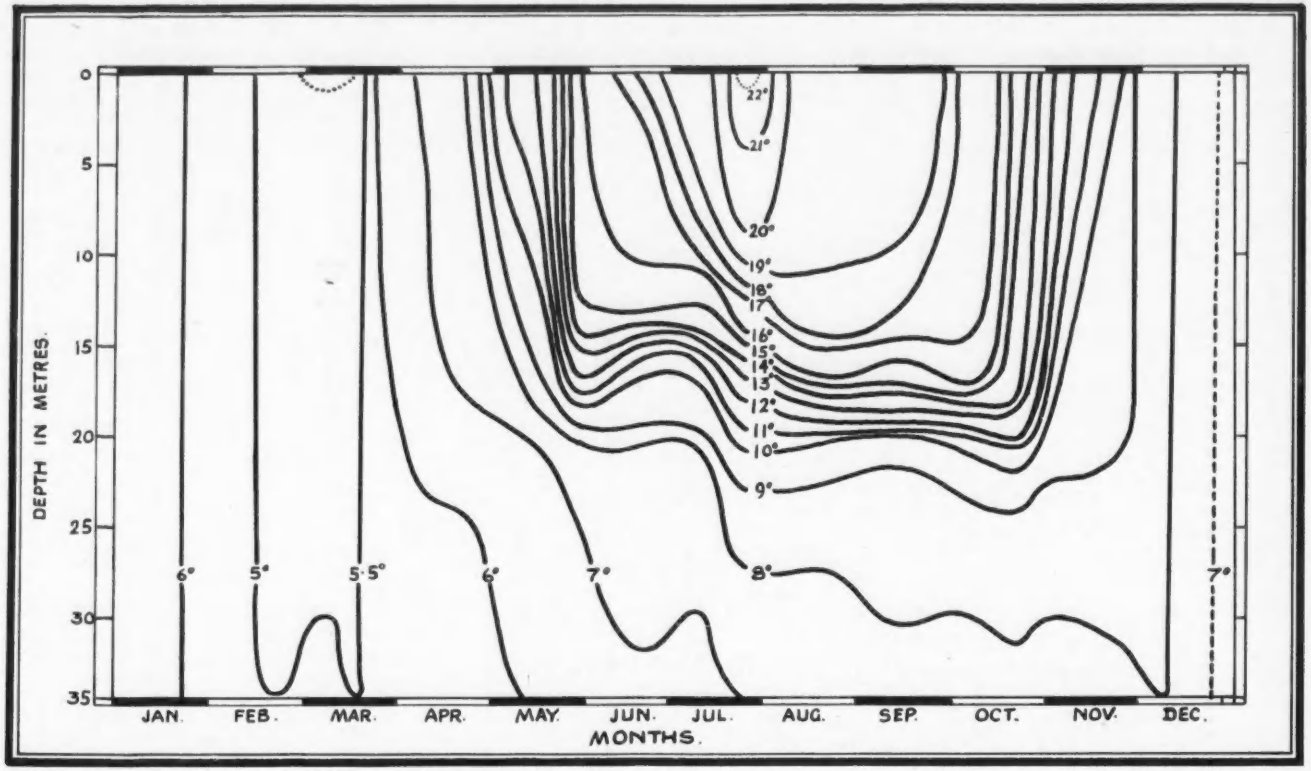

FIGURE 8(*a*). Isotherms (degrees Centigrade) from Cowichan Lake, South Arm, 1938, based upon temperature readings taken at Station I.

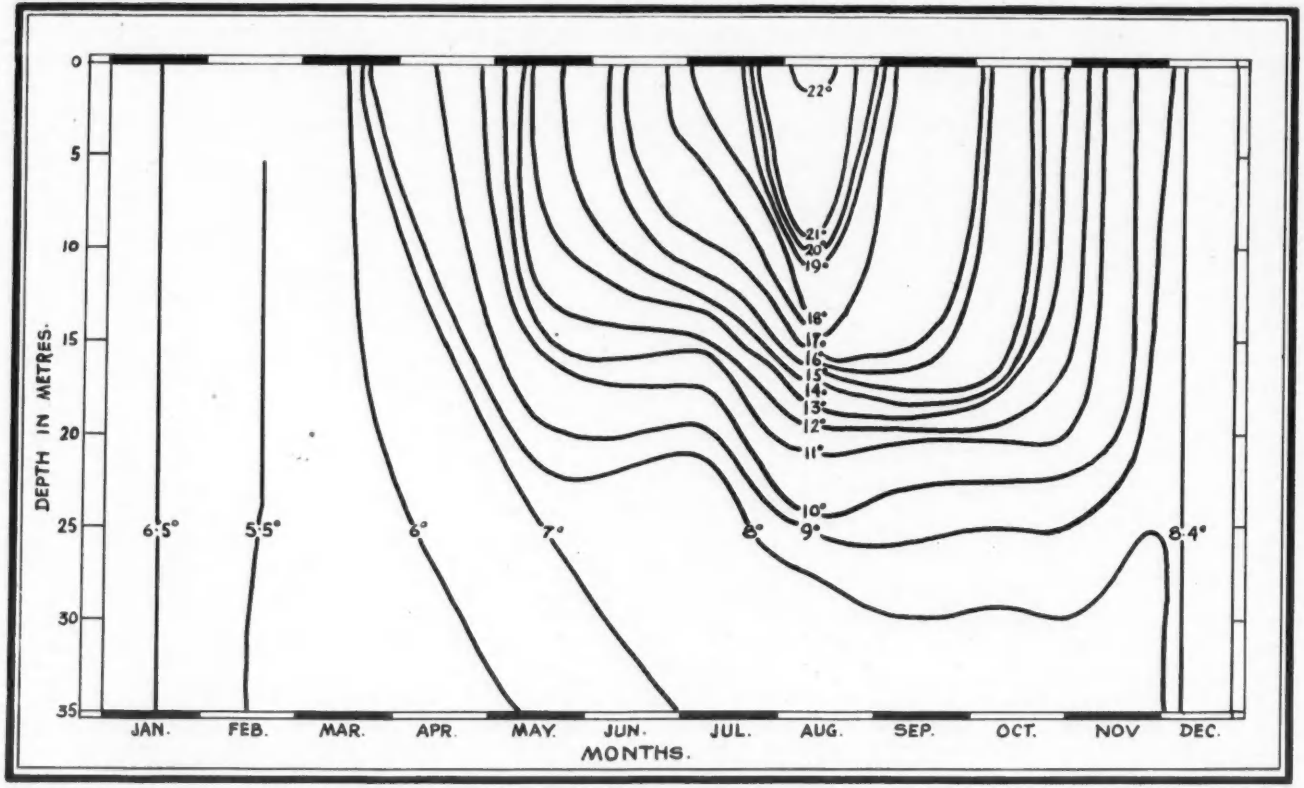

FIGURE 8(*b*). Isotherms (degrees Centigrade) from Cowichan Lake, South Arm, 1939, based upon temperature readings taken at Station I.

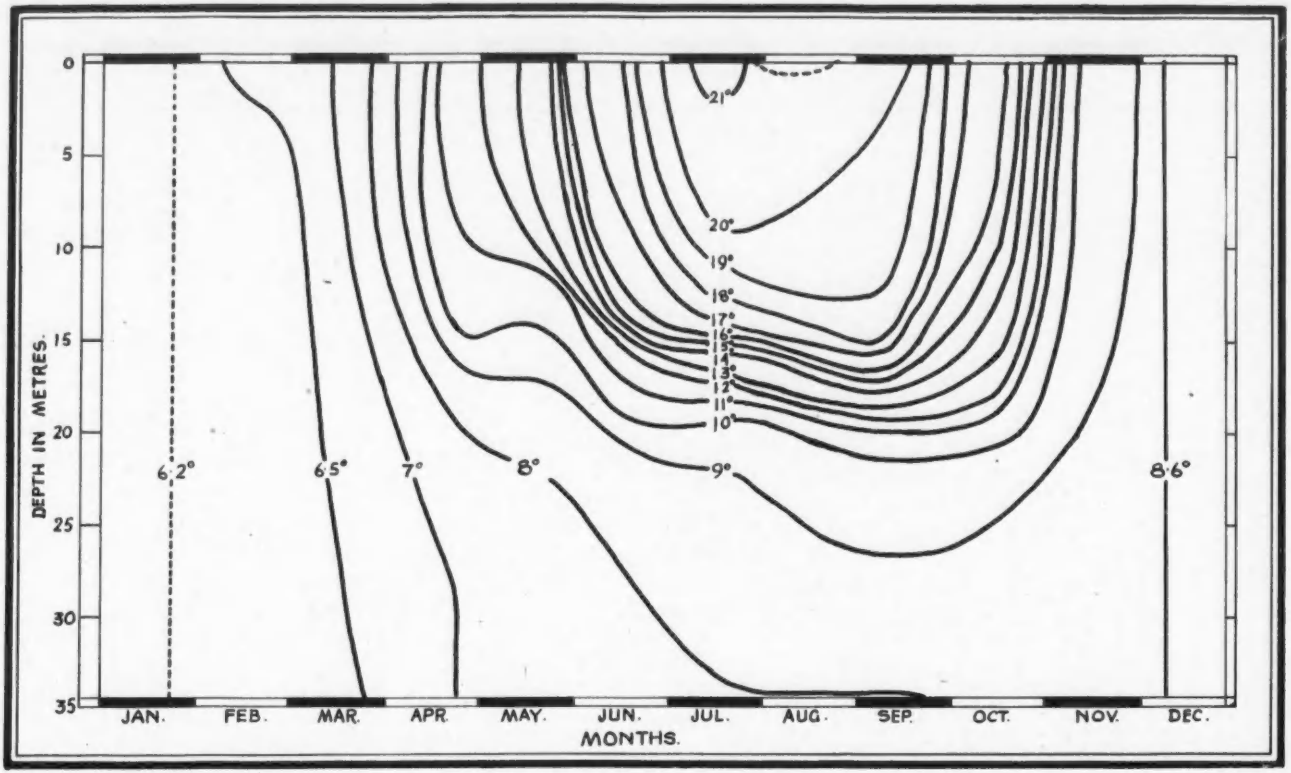

FIGURE 8(*c*). Isotherms (degrees Centigrade) from Cowichan Lake, South Arm, 1940, based upon temperature readings taken at Station I.

years. No doubt part of this heat intake is the result of partial mixing induced by wind action, as may be demonstrated in a later section, but some may be by direct solar radiation, as concluded in the case of Cultus Lake by Ricker (1937). The hypolimnion is rapidly cooled on the establishment of winter circulation.

Annual Variation

To demonstrate the variations in temperature conditions from year to year the temperature trends for surface, 15 metres and 35 metres are shown for Station I in Figures 9-11. It will be seen that, in general, the temperature trends followed the same pattern in 1938, 1939 and 1940, and that the quantity of heat within the lake was greatest during the last year. The lake water was warmer in 1940 no doubt as a result of an unusually warm summer and an exceptionally mild winter.

Wind Direction and Temperature Conditions

It has already been stated that winds have considerable influence on temperature conditions within Cowichan Lake, particularly in determining the time of establishing winter circulation of the water. In summer when the water is stratified, both the vertical and horizontal distribution of the water layers are influenced by strong winds. In the South Arm on several occasions water temperature observations were made at several points extending from the outlet at the east end to Station II at the entrance to the Narrows. From the series of readings taken on two of these occasions (June 24 and July 1, 1937) the distribution of the isothermal layers was plotted. From these data it may be seen that when the wind is blowing down the arm towards the outlet, the warmer layers of water of the lake-surface tend to be driven toward the outlet while when the wind is blowing up the arm of the lake the surface layers are driven toward the Narrows and colder water is forced up at the outlet end. Under the former wind conditions the temperature of the water at the lake outlet was 17.8°C. from surface to bottom (2 metres); under the latter conditions the temperature was 14.8° at the surface and 14.3° at the bottom. Thus the change in wind direction was accompanied by a change of river temperature of about 3°C.

The above observations were made under wind conditions of moderate intensity which had persisted for approximately two hours. It is conceivable that under more extreme conditions disturbances of considerable magnitude may be experienced by the water strata even accompanied by some mixing between the epilimnion and hypolimnion in the near-shore area.

Dissolved Oxygen

Data concerning the amounts of dissolved oxygen in Cowichan Lake are given in Table V. From these figures it is evident that a high oxygen content was present at all times. The lowest value obtained was 3.42 cc. per litre at 35 metres on November 24, 1939, and the deepest sample analysed (110 metres) contained 6.64 cc. of dissolved oxygen per litre.

In general the surface samples at Station I showed an almost saturated and occasionally a supersaturated condition during the season, rarely falling below

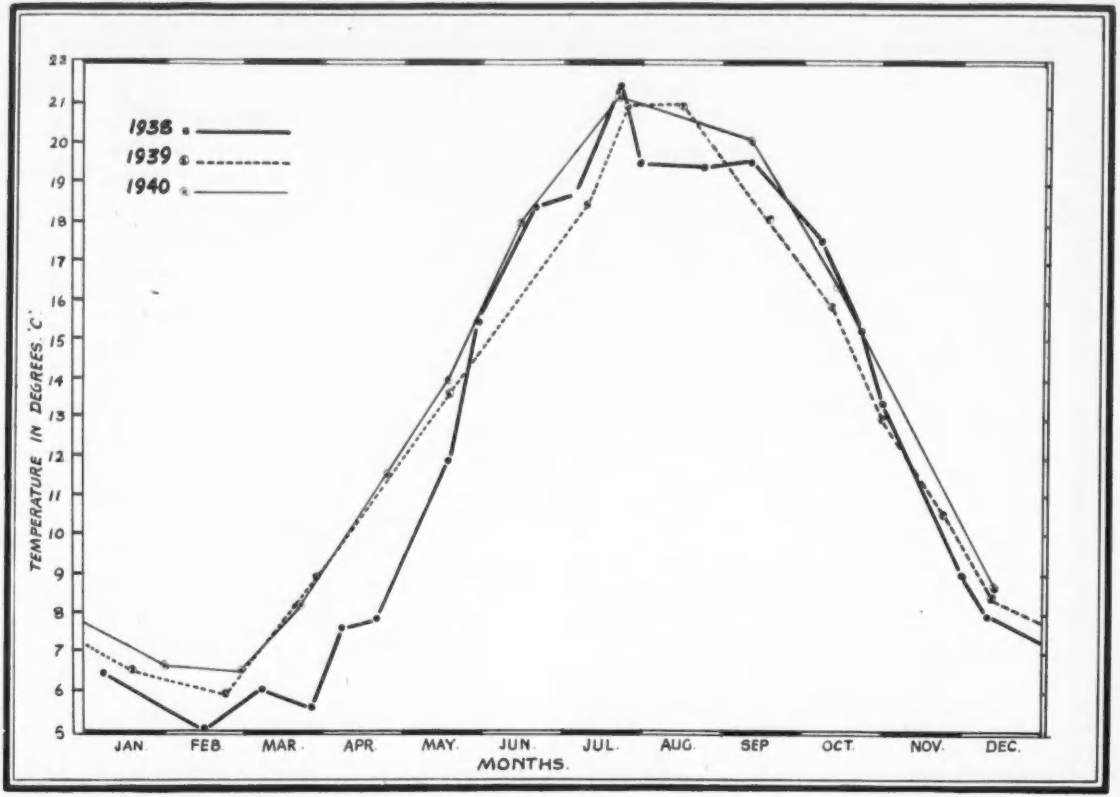

FIGURE 9. Temperature trends of Cowichan Lake at the surface in 1938, 1939 and 1940, Station I.

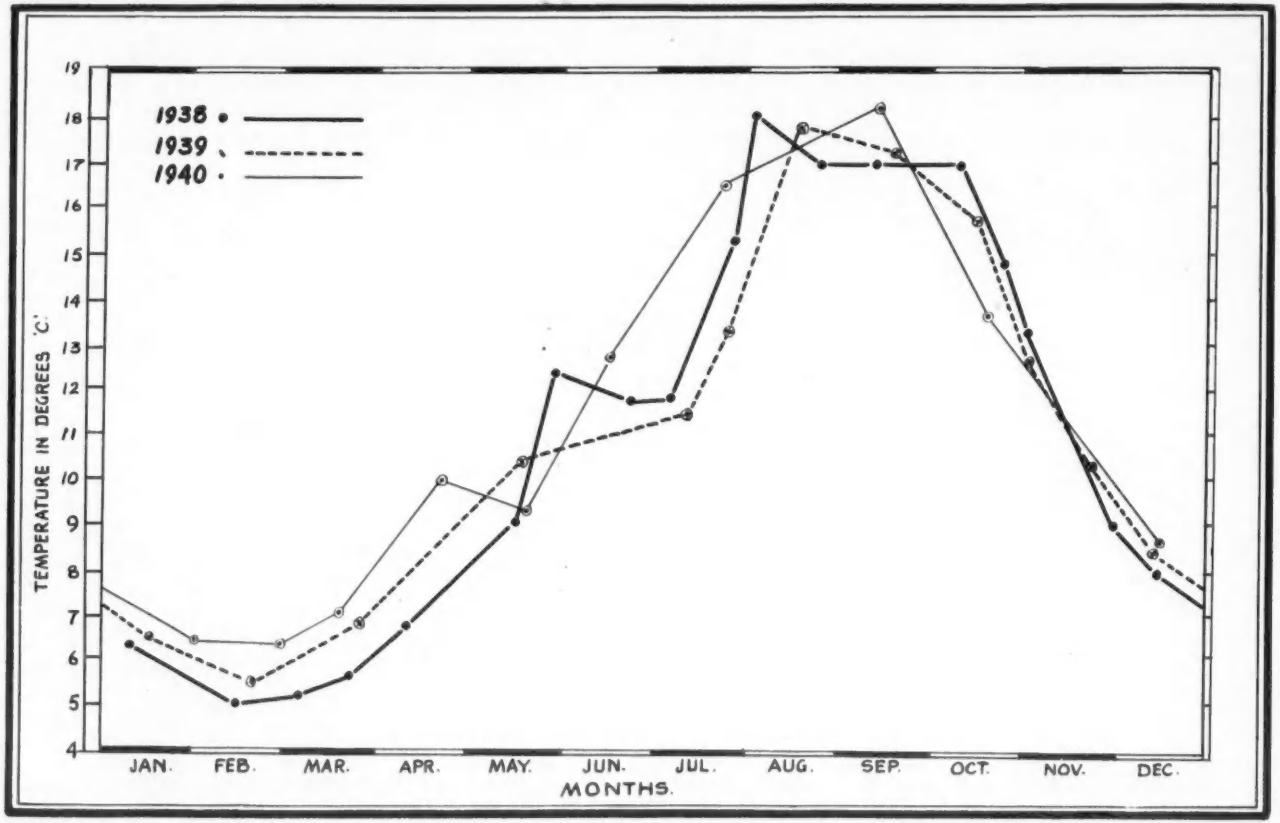

FIGURE 10. Temperature trends of Cowichan Lake at depth of 15 metres in 1938, 1939 and 1940, Station I.

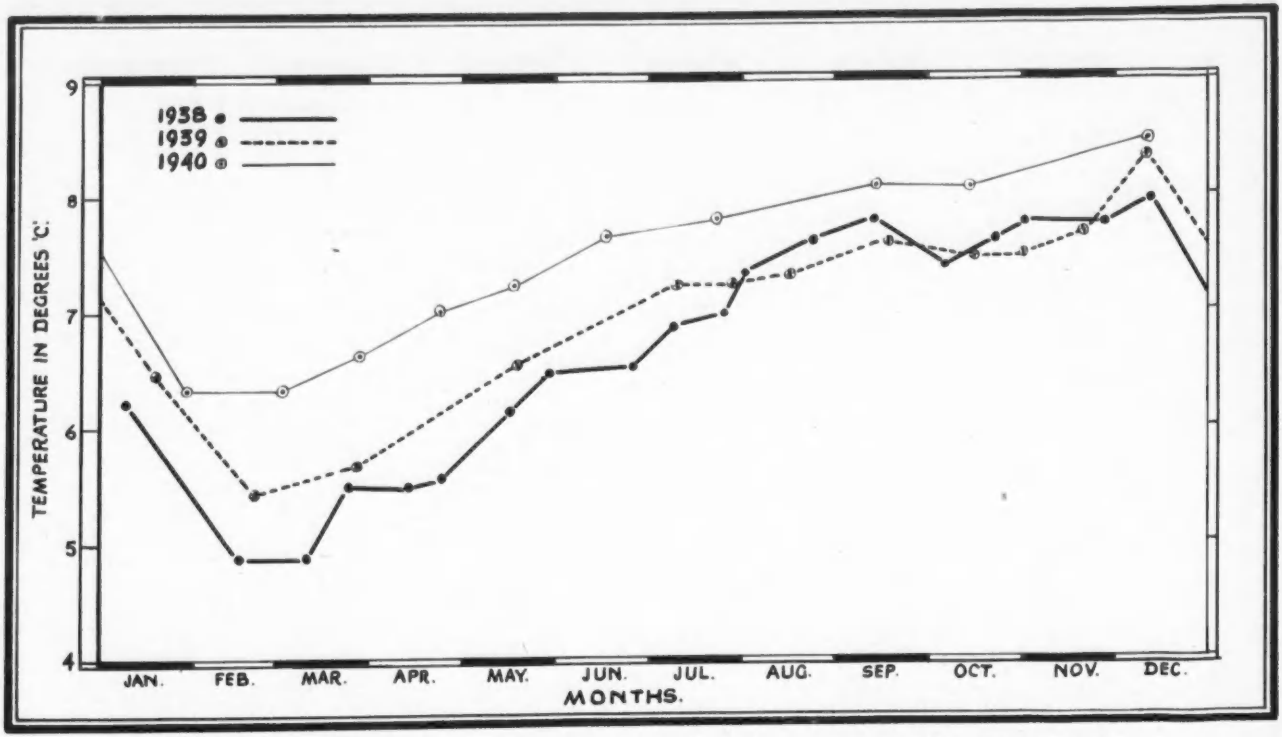

FIGURE 11. Temperature trends of Cowichan Lake at a depth of 35 metres in 1938, 1939 and 1940, Station I.

TABLE V. Dissolved oxygen in Cowichan Lake, in cubic centimetres per litre.

1935	Station I								Station III		Station IV		Station V
Depth (metres)	June 21	July 4	July 11	July 18	July 25	Aug 1	Aug 8	Aug 18	June 27	Aug 16	July 11	Aug 8	July 26
0	5.51	5.77	5.90	5.25	5.25	5.37	5.25	5.24	5.40	5.38	5.13	5.64	5.25
12.5	..	..	..	..	..	..	..	..	..	..	6.03	..	..
35	..	5.73	5.86	5.21	5.34	5.20	5.59	5.33	..	..	6.12	5.59	..
80	..	..	..	..	..	..	..	..	6.51	5.88	..	..	..
110	..	..	..	..	..	..	..	..	..	..	..	..	6.64

1937	Station I															
Depth (metres)	June 17	July 1	July 8	July 16	July 23	July 29	Aug 5	Aug 12	Aug 20	Sept 30	Oct 17	Oct 28	Nov 6	Nov 14	Nov 26	Dec 7	Dec 21
0	6.90	6.90	6.55	5.90	5.77	4.33	4.39	4.32	4.46	4.85	5.12	5.25	5.25	5.37	5.78	6.03	5.89
35	6.54	6.30	6.20	7.03	6.51	4.94	4.68	4.35	4.42	4.68	4.46	4.95	4.17	4.42	3.91	4.55	5.98

1938													
Depth (metres)	Jan 5	Jan 24	Mar 3	Apr 10	May 15	May 29	July 3	July 24	Aug 21	Sept 11	Oct 5	Nov 30	Dec 11
0	6.03	6.16	6.69	7.21	5.77	5.51	4.98	4.83	4.23	4.48	4.60	5.29	5.24
35	..	..	6.32	6.64	5.73	5.86	5.73	5.08	4.74	4.55	4.04	3.90	4.94

1939									1940						
Depth (metres)	Jan 17	Feb 20	Mar 27	May 17	July 26	Aug 15	Nov 24	July 22	Jan 31	Feb 29	Mar 25	Apr 26	May 17	June 14	Sept 11
0	5.57	5.57	6.13	5.13	4.79	4.35	5.51	4.95	5.86	5.98	6.32	6.02	4.12	5.40	5.59
35	5.60	5.79	5.99	5.31	4.71	4.81	3.42	5.40	5.73	6.25	6.25	5.92	5.72	5.59	5.3

TABLE VI. Hydrogen ion concentration of Cowichan Lake water expressed as pH.

1935	Station I								Station III		Station IV		Station V
Depth (metres)	June 21	July 4	July 11	July 18	July 25	Aug 1	Aug 8	Aug 18	June 27	Aug 16	July 11	Aug 8	July 26
0	7.6	7.5	7.4	7.3	7.2	7.2	7.2	7.4	7.5	7.3	7.3	7.3	7.4
12.5	..	..	..	..	..	..	..	..	..	..	7.3	..	..
20	..	..	..	..	..	..	..	..	7.3	..	..	..	..
35	..	6.8	7.1	7.1	7.2	7.1	7.2	6.8	..	..	7.1	7.2	..
80	..	..	..	..	..	..	..	..	7.0	6.8	..	..	..
110	..	..	..	..	..	..	..	..	..	..	..	..	7.3

1937	Station I																			
Depth (metres)	June 17	June 24	July 1	July 8	July 16	July 23	July 29	Aug 5	Aug 12	Aug 20	Sept 19	Sept 30	Oct 7	Oct 17	Oct 28	Nov 6	Nov 14	Nov 26	Dec 7	Dec 21
0	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.8	7.8	7.5	7.8	7.8	7.8	7.8	7.8	7.6	7.6	7.6	7.6	7.8
35	7.0	7.1	7.2	7.0	7.0	7.0	7.0	7.0	6.8	7.0	7.0	7.2	7.2	7.2	7.0	7.1	7.1	7.4	7.3	7.6

1938													
Depth (metres)	Jan 5	Jan 24	Feb 14	Mar 3	Apr 10	May 15	May 29	July 3	July 24	Aug 21	Sept 11	Oct 5	Dec 11
0	7.4	7.4	7.6	7.5	7.8	7.8	7.8	7.6	7.6	7.6	7.2	7.0	7.1
35	7.4	7.4	7.4	7.4	7.5	7.4	7.4	7.4	7.2	7.0	7.0	6.8	7.1

1939					1940						
Depth (metres)	Jan 17	Mar 27	July 8	July 26	Jan 31	Feb 29	Mar 25	May 17	June 14	July 22	Sept 11
0	7.0	7.2	7.1	7.4	7.2	7.2	7.3	7.0	7.1	7.4	7.2
35	7.0	7.2	6.9	6.9	7.2	7.2	7.2	6.9	6.8	6.8	6.6

90 per cent in value. The bottom samples (35 metres) varied between 40 and 90 per cent saturated during the season, the usual value being between 70 and 80 per cent.

The study of the oxygen conditions in Cowichan Lake indicates that this body of water is low in nutritive material (oligotrophic), a condition similar to that found in Okanagan Lake (Clemens, 1939) and Cultus Lake (Ricker, 1937).

Hydrogen Ion Concentration and Bicarbonate Content

Hydrogen ion concentration values, expressed as pH, are given in Table VI. They show that the surface waters of the lake are slightly alkaline, ranging from 7.0 to 7.8 during the season and averaging about 7.4. Samples taken from 35 metres at Station I ranged in value from 6.6 to 7.6, but on the whole were less alkaline than those taken at the surface.

The alkalinity is further indicated by the values of the bicarbonate content. Expressed as mg. per litre of calcium carbonate, these ranged from 18 to 22, the majority of readings being 20 mg. per litre. The results indicate that the bicarbonate content is more or less uniform throughout the lake and is quite low in comparison with other lakes.

BIOLOGICAL CONDITIONS

Plankton

The following organisms have been identified from plankton samples:

GREEN ALGAE: *Staurastrum Avicula* Breb., *Staurastrum gracile* Ralfs., *Staurastrum cuspidatum* de Brebisson, *Staurastrum Artiscon* (Ehr.) Lund., *Xanthidium antilopaeum* var. *polymazum* Nordst, *Micrasterias apiculata* Ehr., *Sphaerocystis Schroeteri* Chod., *Gloeocystis gigas* (Kutz.) Lagerh., *Bulbochaete* sp.

DIATOMS: *Tabellaria fenestrata* (Lyngb.) Kutz., *Tabellaria flocculosa* (Roth) Kutz., *Fragillaria crotonensis* Kitton, *Asterionella formosa* Hass., *Melosira crenulata* (Ehr.) Kutz., *Surirella* sp.

BLUE-GREEN ALGAE: *Coelosphaerium Kuetzingianum* Nig., *Gloeotrichia echinulata* (J. E. Smith) P. Richter, *Nostoc* sp., *Aphanizomenon flos-aquae* (L.) Ralfs.

HETEROKONTAE: *Botryococcus Braunii* Kutz.

PROTOZOA: *Ceratium hirundinella* (F.M.) Schrank, *Dinobryon sertularia* Ehr., *Glenodinium* sp.

ROTIFERA: *Notholca longispina* Kellicott, *Keratella cochlearis* var. *tecta* (Gosse), *Polyarthra trigla* Ehr., *Conochilus* sp., *Ploesoma truncatum* Levander, *Gastropus* sp.

COPEPODA: *Diaptomus oregonensis* Lilljeborg, *Cyclops bicuspidatus* Claus, *Cyclops prasinus* Fischer.

CLADOCERA: *Sida crystallina* (O. F. Muller), *Diaphanosoma brachyurum* (Lieven), *Daphnia pulex* (de Geer), *Daphnia longispina* (O. F. Muller), *Bosmina obtusirostris* Sars, *Eurycercus* lamellatus (O. F. Muller), *Scapholeberis mucronata* (O. F. Muller), *Graptoleberis testudinaria* (Fischer), *Pleuroxus denticulatus* Birge, *Alona* sp., *Polyphemus pediculus* (Linné), *Leptodora kindtii* (Focke).

Of these, only a few occur regularly in samples taken in open water and these include *Tabellaria fenestrata, Asterionella formosa, Coelosphaerium Kuetzinginum* among the plants; *Ceratium hirundinella* and *Dinobryon sertularia* among the protozoans; *Notholca longispina, Keratella cochlearis, Polyarthra trigla* and *Ploesoma truncatum* among the rotifers; *Diaptomus oregonensis* and *Cyclops bicuspidatus* among the copepods and *Diaphanosoma brachyurum, Daphnia longispina* and *Bosmina obtusirostris* among the Cladocera.

In order to determine the relative numbers of plankton organisms present in the lake at different seasons and at different depths a series of samples was taken in 1940 at Station I by means of a plankton trap of 10 litres capacity. The organisms so collected were counted in the following manner. The original sample as collected by the trap was concentrated by drawing off excess water by means of a pipette screened with Number 20 bolting silk to prevent the loss of plankters, and all the organisms were then transferred to a counting cell. In most cases each individual was counted, but when the numbers rendered this difficult only those within a portion of the counting cell were enumerated. The results of these counts are on file at the library of the Pacific Biological Station; a summary is given as follows:

COPEPODA

Diaptomus. Apparently present all year round. Reached a peak of abundance (5.14 per litre) in June.

Cyclops. More numerous than *Diaptomus.* Apparently two peaks of abundance, spring and fall, as was found by Ricker in Cultus Lake.

Nauplii of both *Diaptomus* and *Cyclops.* Present in considerable numbers in all samples taken. Two major peaks of abundance are conspicuous, in early spring and early fall. It is interesting to note that in 1940 the spring peak of the nauplius population is followed by peaks in both *Diaptomus* and *Cyclops* whereas the fall nauplius peak is followed by a rise in numbers of *Cyclops* only, which suggests that the autumn nauplius population is mostly of this genus.

CLADOCERA

Daphnia. Less important than either of the copepods in point of numbers. A single major peak (1.58 per litre) occurred in mid-June. The figures obtained are probably lower than the true values because *Daphnia* may actively avoid capture by the plankton trap.

Bosmina. Apparently less numerous than *Daphnia.*

Diaphanosoma. Present only on a few occasions.

ROTIFERA

Keratella. The most abundant rotifer, reaching 2.34 individuals per litre in July.

Notholca. Present in numbers in samples taken in early summer only.

Polyarthra. Similar to the former but present in fewer numbers.

PROTOZOA

Dinobryon. Apparently absent in the January samples; present in all others in numbers reaching "bloom" proportions during the months of May, June and July.

Ceratium. Present in some numbers at all times, apparently most abundant in mid-winter (1.91 per litre). At no time during the year was this organism as numerous as reported in Cultus Lake.

DIATOMS

Asterionella. Colonies were present in all samples with indications of a "pulse" occurring in April and in June. The maximum number recorded is low as compared with Ricker's figures (55 colonies per litre in Cowichan Lake compared with 10,000 colonies per litre in Cultus Lake).

Tabellaria. A great increase in numbers of individuals is indicated by samples taken in September and again in December.

BLUE-GREEN ALGAE

Coelosphaerium. Occurred suddenly in samples collected in June and was present also in July.

The number of species found in the plankton (44) compares favourably with the numbers found in Cultus Lake (41) but the quantity appears to be much smaller than that produced by Cultus Lake. The material available does not permit an accurate comparison being made but in the case of each species, except *Dinobryon*, the maximum counts made of the Cowichan Lake trap plankton in 1940 are far below those recorded for Cultus Lake (Ricker, 1938). While the results of a single year's sampling cannot be accepted as conclusive they indicate that the plankton productivity of Cowichan Lake is low.

BOTTOM ORGANISMS

Bottom samples were taken by means of an Ekman dredge. There are 38 collections taken from various parts of the lake during June, July and August of 1935.

ALGAE

Nostoc. Small colonies ranging from about 1 mm. to 10 mm. in diameter in all but the deepest samples, mostly in early summer. The colonies were often attached to some support but many were free on the bottom.

Nitella. Occasionally found in shallow water, particularly near the lake outlet.

Chara. Sometimes found associated with *Nitella.*

PORIFERA

Spongilla sp. Occasionally common in shallow water.

TURBELLARIA

Planaria sp. A few specimens were found on gravelly shores and occasionally in deeper water.

CHAETOPODA

Oligochaeta—Two species of aquatic worms were found; one belonging to the genus *Stylaria*, the other to the Family Tubificidae. The latter species was occasionally abundant in deep water.

HIRUDINEA

Glossiphonia sp. Numbers of these small leeches carrying young were found in one or two dredgings in moderately deep water (8 m.). A few individuals of another unidentified species were also collected and occasionally egg-cases were found attached to shells of fresh-water mussels (*Anodonta*).

CRUSTACEA (AMPHIPODA)

Hyalella azteca Saussure. This small amphipod was fairly abundant and well distributed, individuals being found in almost all samples of bottom mud. In a few cases it was the most abundant organism found.

Eucrangonyx gracilis (Smith). Only one individual of this species was collected; it was associated with the ivy-leaf duckweed (*Lemna trisulca*) in shallow water.

INSECTA

Except for the deep-water chironomids, the insect population of the lake was found to be scanty. This paucity of insects is probably connected with the scantiness of bottom vegetation since most aquatic organisms of this type usually associate themselves with water plants both for food and protection.

Trichoptera—Several unidentified species represented by both larvae and pupae, together with a few individuals of the genus *Hydropsyche*, represented the caddisfly population of the lake. In a few instances towards the end of the summer large numbers of old cases were found, indicating a pervious emergence of the adults.

Plecoptera—Stonefly nymphs were rarely found in the lake during the investigation. At the beginning of each season a small emergence of adults was noted particularly near the river.

Odonata—Dragonfly nymphs were not commonly found in the lake. The few that were collected were found associated with water plants in shallow water. Nymphs of the damselfly (*Enallagma*?) were also found in the same habitat.

Ephemeroptera—Nymphs of mayflies were found only rarely in the lake.

Diptera—Chironomidae. The aquatic larval stages of midgeflies were the most common insects found in the dredgings. In most cases they were confined to the deeper parts of the lake; in only a few instances were they found in water shallower than 5 metres. The numbers of chironomid larvae showed a decrease toward the end of the season, presumably due to the emergence of adults.

Tipulidae—Two or three larvae of craneflies were found during the summer.

Coleoptera—Gyrinidae. Several larvae of a whirligig beetle were collected in shallow water.

ARACHNIDA

Hydracarina. Water mites were occasionally taken in dredgings.

DISCUSSION

Two series of dredgings spaced at an interval of five weeks were taken near Station I in the South Arm of the lake. If these samples are accepted as being

representative they show a variation in numbers of bottom organisms coincidental with the progress of the season as demonstrated by Table VII. The change in population is best shown in the case of the chironomid larvae and oligochaetes both of which showed a decided decrease in numbers toward the end of the season. The disappearance of the chironomids is no doubt due to the emergence of adults during the summer. The disappearance of the oligochaetes may be the result of natural mortality or predation. Other organisms such as *Hyalella* and *Nostoc* show less significant fluctuations in population, their numbers probably varying with different stages in life-history.

TABLE VII. Variation in numbers of bottom organisms off Station I from July 9 to August 18, 1935. Figures represent the number taken in one dredging of 500 square centimetres.

	1 metre		2 metres		7 metres		40 metres	
	July	Aug	July	Aug	July	Aug	July	Aug
Chironomids	2	1	3	0	3	0	14	1
Oligochaetes	4	1	3	0	2	0	10	0
Caddis	1	0	0	1	1	0	0	0
Gyrinids	0	1	1	2	0	0	0	0
Menetus	4	3	3	0	1	1	2	1
Pisidium	2	2	3	0	2	2	2	1
Anodonta	3	0	0	1	1	0	0	0
Hyalella	16	3	4	5	7	5	0	0
Nostoc	20	0	many	3	many	16	0	0

Table VII also indicates to some extent a distribution of numbers according to the depth. Certain organisms such as chironomids and oligochaetes appear to prefer the deeper water while others, such as *Hyalella*, prefer the shallows. The distribution of the mollusc *Pisidium* seems independent of both depth and season.

Similar dredgings taken in other parts of the lake showed a population of bottom organisms very similar to that of the South Arm in both kinds and numbers. In general the bottom fauna of Cowichan Lake is rather scanty. Although a fair variety of forms occur none can be said to be abundant.

MOLLUSCA

The following list is based on shells in the Hanham collection now in the Provincial Museum (indicated by the symbols HC), and on more recent specimens identified by Mr. John P. Oughton, formerly of the Royal Ontario Museum of Zoology, Toronto.

Univalves

Physa coniformis Tryon. Small pond, Cowichan River Road. (HC)

Physa carltoni Sea. Small pond, Cowichan River Road, October 1925 (HC)

Physa gabbi Tryon. Quamichan Lake. (HC)

Physa blandi Sea. Cowichan River. (HC)

Physa sp. cf. *distinguenda* Tryon and *occidentalis* Tryon. Cowichan Lake, August 6, 1944. Common near shore and occasionally in deeper water.

Stagnicola lepida Gould. Quamichan Lake. (HC)

Stagnicola proxima rowellii (Tryon) Quamichan Lake and Cowichan River. (HC)

Planorbis hornii Tryon. Quamichan. (HC)

Lymnaea stagnalis L. Quamichan Lake; Cowichan Lake, August 6, 1944. Rocky shores in shallow water.

Lymnaea palustris Muller. Quamichan Lake. (HC)

Helisoma trivolvis (Say). Cowichan Lake, August 6, 1944. Fairly common at moderate depths.

Menetus opercularis planulatus (Cooper). Cowichan Lake, August 6, 1944. Also common at moderate depths.

Bivalves

Pisidium variabile Prince. Cowichan River. Fairly common at all depths.

Musculium lacustre Muller. Cowichan River. (HC)

Musculium ryckholti raymondi (Normand). Duncan, B.C. (HC)

Anodonta beringiana Midd. Cowichan Lake and river. Occasionally abundant in muddy bottom both near shore and in deeper water.

AQUATIC PLANTS

Although aquatic plants were relatively few in both numbers and kind, they were abundant in a few small areas. These more productive spots were usually located in small bays or along shallow shores where accumulated snags allowed a muddy bottom to exist. In such protected localities the following plants were found:

Potamogeton amplifolius Tuckerm. Large-leaved pondweed
Potamogeton epihydrus var. *Nuttallii* C. & S.
Potamogeton Robbinsii Oakes. Robbin's pondweed
Potamogeton Richardsonii (A. Benn.) Richardson's pondweed
Ranunculus aquatilis L. Water buttercup
Myriophyllum verticillatum L. Water milfoil
Nuphar polysepalum Engelm. Common water lily
Lemna trisulca L. Ivy-leaved duckweed
Juncus supiniformis Engelm. (?) Hair-leaved rush
Fontinalis antipyrectica var. *patula* (Card) Grout. Water moss
Equisetum limosum L. Horsetail
Lobelia Dormanii L. Water lobelia
Nitella sp.
Chara sp. Stonewort
Menyanthes trifoliata L. Buckbean

The following aquatic plants have been introduced by Mr. Buchanan Simpson in the Marble Bay area:

Nymphaea alba L.
Nymphaea alba var. *rosea* (Lonnv.)
Iris pseudacornis L.
Iris versicolor L.

FISHES

Since the salmonoid fishes of the Cowichan system have already been discussed (Neave, 1949) the following notes refer to species not dealt with in that report.

Entosphenus tridentatus (Gairdner). Pacific Lamprey. The sea lamprey appears to be abundant in the Cowichan Lake and River system where during one stage of its life it preys upon the game fishes to a serious extent. Adults apparently ascend the river during the summer months; specimens were seen or collected at Skutz Falls on August 22, August 27 and September 1, 1937. Recently hatched larvae, presumably of this species, were taken in plankton nets in the river at the Hatchery on June 27, 1937. Larger larvae ranging in size up to four inches in length, were taken at various times during the summer months in silt deposits of the river. Following a non-parasitic larval stage of undetermined length these lampreys metamorphose, and then appear to remain in fresh water for an indefinite time to prey upon game fish. During this phase of their life-cycle they average about 8 inches in length.

The numbers of lampreys in Cowichan Lake appear to be considerable. Although they are not often seen by anglers, since they usually leave the host fish before being netted, approximately 8 out of 10 fish taken bear fresh or old scars resulting from lamprey attack. Occasionally lampreys remain attached to trout until the fish has been brought into the boat; reports of three fastened to one fish have been received.

The following is a record of an 8-inch lamprey taken from a captured trout on October 6, 1937, and placed in a Hatchery tank containing three cutthroat trout measuring from 10 to 12 inches in length.

October 14th. Lamprey still unattached but active when disturbed.
October 15th. Lamprey attached to 12-inch cutthroat on right shoulder above lateral line and immediately behind operculum.
October 22nd. Fish free of lamprey; prominent scar visible.
November 22nd. Lamprey still unattached. Two Dolly Varden char and one coho jack placed in tank.
November 28th. Lamprey observed attached to coho.
March 4th, 1938. Lamprey found dead and partly decomposed.

During July, 1937, a brown trout to which a lamprey was attached was observed over a period of several weeks in the pool at the Hatchery boathouse.

It would appear from these observations that lampreys remain attached to the host for some considerable time and also live unattached for varying periods. Whether or not the lamprey of the Cowichan River system descends to the sea is not known.

Specimens of *E. tridentatus* from the Cowichan system have been examined by Dr. C. W. Creaser of Wayne University and Dr. Carl L. Hubbs of the Scripps Institute of Oceanography, who state that the specimens examined apparently represent a dwarfed race.

Lampetra planeri (Bloch.). Brook lamprey. This is a non-parasitic species known to occur in Holmes Creek, flowing into Somenos Lake; it probably also occurs in other streams of the Cowichan system.

Lampreys of this species were first observed spawning by the writer on May 8, 1939, about 100 yards below the falls in Holmes Creek. Local residents reported them to be present as early as the third week in April and to have appeared about the same time for the previous five years at least.

Fertilized eggs, collected on May 8, 1939, hatched in about 28 days in water varying in temperature from 10 degrees to 12 degrees Centigrade. On several occasions following this spawning period larvae were collected below the redds in silt pockets of the stream-bed.

Ameiurus nebulosus (LeSueur) Brown catfish. Catfish are abundant in Somenos Lake near Duncan where they were apparently introduced sometime after 1906 when they were first imported to Vancouver Island. They are sometimes taken in Cowichan River near the mouth of the stream draining Somenos Lake but do not seem to have made their way into other tributaries as yet.

Cottus asper Richardson. Sculpin. The sculpin or bullhead is abundant, particularly in the pools of the river and along certain portions of the lake shore. Individuals range in size up to about five inches in length with an average of approximately three and one-half inches.

A series of post-embryonic larvae and fry ranging in size from 6.4 mm. to 22.2 mm. in length were collected by plankton net in the river at the hatchery between June 15 and 26, 1939.

Sculpins form a minor part of the diet of Cowichan River cutthroat and brown trout (Idyll, 1942).

Gasterosteus aculeatus L. Stickleback. Sticklebacks are abundant throughout the Cowichan system mainly in backwaters of the river, sloughs, and shallow, weedy portions of the lake shore. The spawning period is very prolonged, extending from about the first week of April to the first week of September (1940) judging by nest-building activities observed at these periods. The rate of growth is rapid; fish averaging 7 mm. in length at hatching attained the following lengths at stated periods: 16.5 mm. (1 month); 22.2 mm. (2 months); 33.4 mm. (3 months); 44.8 mm. (4 months); 63.8 mm. (10 months). They apparently are ready to breed before the completion of the first year.

Plankton provides the chief source of food. Examination of stomach contents of 28 adults gave the following percentage occurrences: Cladocera, 95; copepods, 90; insects, 25; ostracods, 4; amphipods, 7; and algae, 7.

Idyll (1942) reports that sticklebacks are one of the principal foods eaten by cutthroat and brown trout in the Cowichan River.

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Principles Affecting the Size of Pink and Chum Salmon Populations in British Columbia

By Ferris Neave

Pacific Biological Station, Nanaimo, B.C.

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ABSTRACT

In pink salmon (*Oncorhynchus gorbuscha*) the survival during the freshwater phases of the life-cycle has been found to vary from about 1 to 24 per cent of available eggs. Natural survival during marine existence is considered to average about 5 per cent. In the central region of the British Columbia coast the annual catch averages about 60 per cent of the adult fish. Populations maturing in "even" and "odd" years vary in size independently. Fluctuations in level of stock originate mainly in fresh water.

Population levels and changes are determined by the combined effects of three types of mortality: (*a*) mortality which becomes relatively heavier as populations increase in density (*compensatory*); (*b*) mortality which becomes relatively heavier as populations decrease in density (*depensatory*); (*c*) mortality which is independent of density (*extrapensatory*). Compensatory mortality is especially identified with the period of spawning and incubation. Depensatory mortality is considered to occur mainly during the period of fry migration and to be due to predation. Extrapensatory mortality may occur at any stage; it is most variable during the period between entrance of the adults into fresh water and emergence of the free-swimming fry.

Populations of chum salmon (*O. keta*) are controlled by similar influences. Effects are modified by higher egg-production and a less rigid life-span than in the pink salmon.

INTRODUCTION

The various species of Pacific salmon (*Oncorhynchus* spp.) exhibit changes in abundance which may be of an annual character or may be associated with longer time periods. Such changes are of general interest because they represent phenomena which in some form and at some time are common to all species of animals and indicate the terms on which populations continue to exist. They are also of specific practical interest because the fortunes of a large industry depend upon both the short-term and long-term abundance of these fish.

The present study represents part of a broader investigation undertaken under the auspices of the Fisheries Research Board of Canada, with the general object of acquiring information necessary for (*a*) the prediction of changes in abundance of Pacific salmon, (*b*) the maintenance or increase of the stocks of these fish available for sustained exploitation.

The purpose of the account presented here is to examine the general factors determining population size in two of the five species of Pacific salmon occurring in British Columbia, with particular reference to the above-mentioned problems of prediction and practical remedial action. These two species (the pink salmon, *Oncorhynchus gorbuscha*, and the chum salmon, *O. keta*) are sufficiently similar in life-history and distribution to facilitate a common investigation. At the same time they exhibit certain differences in the details of behavour, life-history and fecundity which help to elucidate general principles applying to both species.

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I. PINK SALMON
Oncorhynchus gorbuscha (Walbaum)

The pink salmon is generally distributed throughout the length of the British Columbia coastline. In fresh water it is scarce in certain areas of both east and west coasts of Vancouver Island. Elsewhere, the numbers of adults in alternate years may be small. With these provisos it is the most abundant salmon in British Columbia.

The adults enter fresh water mainly in August and September, utilizing both large and small streams. In moderately large unobstructed rivers such as the Bella Coola they may travel upstream for as much as fifty to seventy miles, while in the Skeena watershed many thousands annually ascend the Babine River to a distance of nearly 400 miles (by water) from the ocean. In general, however, a great part of the spawning takes place close to salt water, sometimes beginning within the limits of tidal influence. Deposition of eggs occurs mainly in September and early October. In observed instances the hatching of the alevins is completed during February and the emergence of the fry from the gravel, followed by their immediate migration to salt water, reaches a peak at the end of April or early in May. The young fish can be observed feeding in schools at or near the surface of the sea in May and June, when they may already be found at a distance of many miles from their presumed natal streams. With the advancing season they appear to disperse somewhat and to descend to a depth which, combined with their increased size and activity, makes capture difficult (observations of writer and others in Strait of Georgia). Their subsequent marine distribution is not ordinarily witnessed until the summer of the following year, when the maturing fish begin to be taken in July by the fishery.

So far as is known, the total life-cycle invariably occupies two years.

Egg-Production

Since changes in the size of any population are determined by the birthrate and the deathrate, the number of eggs produced is of basic importance to the present discussion. Total egg-production is obviously a product of the average egg-production per female and the number of females in a population.

Available data on the average production of eggs by female pink salmon are shown in Table I.

From these figures it appears that (1) the general average egg-production per female in pink salmon is about 1,700, which is lower than that of any other species of Pacific salmon; (2) differences in average number of eggs occur between different localities, and in the same locality in different years.

The first point carries the obvious implication that if the species is to maintain itself the mortality occurring during the life-cycle (from egg to spawning adult) must be less than in the other species of *Oncorhynchus*. If we assume an average egg-production of 2,700 per female *chum* salmon (see p. 480), with equality of sexes, then a total mortality of 99.926 per cent applied to the product of a spawning pair would just permit replacement of the parents. The application of the same mortality rate to pink salmon eggs (taking an average of 1,700) would re-

duce the spawning stock to less than one quarter of its original size in three generations. To maintain stability it would be necessary to apply a mortality rate of 99.882 per cent to the pink salmon. This latter rate would permit a chum salmon spawning stock to triple itself in two generations. A steady state would of course be represented in either instance by: $M = \frac{100\ (E-2)}{E}$, where M is percentage total mortality and E is the average number of eggs per spawning female.

It does not follow that if the average egg-production of either species were changed, the mortality rate at present characteristic of the species would remain unaltered. It does follow, however, that if average egg-production remains constant, a change of a small fraction of 1 per cent in the total mortality rate would quickly produce a spectacular increase or decrease in the spawning stock. Hence the average egg-production per female of a population which is maintaining a fairly constant level over a prolonged period, must be a very sensitive measure of the mortality which is actually prevailing.

TABLE I. Average egg content of pink salmon.

Locality	Year	Number of fish	Average number of eggs	Authority
McClinton Creek	1930	97	1535	Pritchard (1948a)
	1932	73	1758	" "
	1934	165	1799	" "
	1936	91	1899	" "
	1938	40	1698	" "
	1940	41	1619	" "
Morrison Creek, V.I.	1943	38	1779	Pritchard (unpublished)
	1945	27	1862	Neave (unpublished)
Namu	1934	41	1841	Foerster & Pritchard (1936)
Fraser River	1934	48	1755	Foerster & Pritchard (1936)
Port John	1947	38	1520	Hunter (unpublished)
	1950	20	1593	" "

While these considerations can be applied to long-term averages, considerable variation in egg-production is apparent from generation to generation and from place to place. In so far as topographic differences remain constant, they must reflect local differences in mortality rate or active changes in population size. Variations in fecundity from generation to generation may, however, merely represent fluctuations around an average. Pritchard's (1948a) figures for average egg counts in a series of consecutive generations of a pink salmon population range from 1,535 to 1,899. This represents a fluctuation of about 11 per cent above or below the overall mean of 1,718. Such a variation is certainly far from insignificant but it is evident that other major factors must be found to account for the much greater variations which occur in the size of pink salmon populations.

Sex Ratio

The sex ratio should be considered in attempting to define the factors which may affect population size, since any continued inequality between the sexes would have to be taken into account in determining reproductive efficiency.

The percentage of each sex recorded in the spawning escapement to various streams is shown in Table II.

Table II. Sex ratio (per cent) of pink salmon escapements.

Locality	Year	Number of fish	Males	Females	Authority
McClinton Creek	1930	66,153	49.8	50.2	Pritchard (1948a)
	1932	15,600	51.3	48.7	" "
	1934	155,196	49.9	50.1	" "
	1936	52,312	46.3	53.7	" "
	1938	10,577	52.5	47.5	" "
	1940	35,521	53.7	46.3	" "
	1942	36,893	47.6	52.4	" "
Morrison Creek, V.I.	1943	15,755	48.6	51.4	Pritchard (unpublished)
	1945	13,411	52.0	48.0	Neave (unpublished)
Hooknose Creek	1947	5,576	47.1	52.9	Hunter (unpublished)
	1948	1,160	48.5	51.5	" "
	1949	1,173	55.4	34.6	" "
	1950	1,857	44.7	55.3	" "

These figures do not vary consistently in one direction and for the most part the deviation from equality is small. The tabulated values refer to populations remaining after the operation of a fishery which has been thought to be sometimes selective in respect to sex of fish caught. The figures do not indicate any marked selectivity unless the latter has acted in such a way as to balance an initial inequality in the production of the sexes.[1] However, Robertson (1951) in a sample of 232 migrating pink salmon fry at Hooknose Creek, found 52 per cent males and 48 per cent females—a difference which is insufficient to suggest a general departure from a 50-50 ratio.

Although selective fishing may introduce local inequality at times, it is provisionally assumed that both the young fish and the spawning populations tend to have an equal division of the sexes. The complications introduced by the presence of "jacks" (precocious males) do not arise in the case of the present species.

Mortality

Since the birthrate can be regarded as relatively constant, major changes in population size must be ascribed to changes in mortality.

It is convenient to divide the total mortality which attends the life-cycle into

[1]At the present time about 70 per cent of the annual British Columbia catch of pink salmon is taken by purse seine, a method which is assumed to be non-selective for sex.

three categories, namely: freshwater mortality, natural ocean mortality and fishing mortality.

For practical purposes these categories correspond to consecutive portions of the life-history, since pink salmon fishing is almost entirely confined to a short period at the close of the ocean phase of existence.

FRESHWATER MORTALITY AND SURVIVAL

1. *Total freshwater survival.* Counts or quantitative estimates of the number, sex ratio and egg content of adult pink salmon migrating up certain streams, and of the number of young migrants subsequently descending to the sea, have been made at several localities over varying periods of time, utilizing weirs and pens for trapping the fish. The total number of eggs carried upstream by a given spawning run has been estimated by sampling an appropriate number of females throughout the period of the upstream migration and has usually been termed the "potential egg deposition". The number of young fish recorded as sea-going migrants has been expressed as a percentage of the potential egg deposition, thus representing the "reproductive efficiency" or percentage survival between these two points in the life-cycle.

The operation of counting weirs is attended by difficulties, most of which are connected with sudden large increases in the volume and speed of the water flow. Enforced suspension of counting for short periods has been a not infrequent occurrence in the history of some installations of this kind, necessitating a certain amount of interpolation. The possible errors resulting from such lacunae

TABLE III. Freshwater survival of pink salmon. Fry entering the sea expressed as percentage of potential egg deposition.

Locality	Brood year	Survival (%)	Authority
McClinton Creek	1930	10.6	Pritchard (1948)
	1932	17.4	" "
	1934	9.0	" "
	1936	6.9	" "
	1938	23.8	" "
	1940	19.0	" "
	Geometric mean	13.15	
Morrison Creek, V.I.	1943	4.7	Pritchard (unpublished)
	1945	6.7	Neave (unpublished)
Hooknose Creek	1947	0.87	Hunter (1948)
	1948	8.02	" (1949)
	1949	6.24	(unpublished)
	1950	15.11	" "
	Geometric mean	5.07	
Sashin Creek, Alaska	Geometric mean for 1940–50	1.16	U.S. Fish & Wildlife Service*

*The writer is indebted to M. G. Hanavan, Acting Chief, Alaska Fishery Investigations, for these figures which are of great interest for comparative purposes.

have been discussed by Pritchard (1948a) with reference to the series of experiments conducted by him at McClinton Creek. Somewhat similar considerations apply to certain other cases. The figures obtained by careful and competent investigators are accepted here as being the best possible estimates and as being very close to the true values. They are basic to the consideration of factors causing changes in abundance of pink salmon.

From published records and through the courtesy of investigators in making their unpublished results available, the figures presented in Table III have been compiled.

The geometric mean of the recorded freshwater survival for each of the three streams for which several years' data are available, is as follows: McClinton Creek, 13.15 per cent; Hooknose Creek, 5.07 per cent; Sashin Creek, 1.61 per cent. These differences are large and can be considered to be statistically significant ($P<.05$). Evidently these populations are not being subjected to the same conditions of environmental pressure.

These different average survival rates may have a profound effect not only on the absolute number of sea-going migrants but also on the magnitude of the fluctuations between different generations of such migrants. Evidently if a population is subject to an average freshwater mortality of 86 per cent, a variation of as much as 7 per cent in either direction (79 to 93 per cent) will only increase or reduce the output by 50 per cent. On the other hand, with an average mortality of 98 per cent a shift of only 2 per cent in the mortality rate would double the output or eliminate it entirely. The following comparison shows the effects of the recorded ranges of freshwater mortality as applied to the offspring of a pair of fish producing 1,700 eggs.

Stream	Observed mortality range (%)	No. of migrants produced (*a*) Maximum	(*b*) Minimum	Ratio of (*a*) to (*b*)
McClinton	76.2 – 93.1	404	118	3.45:1
Hooknose	85 – 99.1	255	15	17.00:1
Sashin	95.6 – 99.8	109	3.4	32.00:1

It appears that a much greater relative range of fluctuation (as measured by the reproductive success of individual pairs of fish) can be expected in streams in which the average survival rate is low.

2. *Immediate causes of death.* Many more or less specific causes of loss can be recognized as contributing to the total mortality experienced in the freshwater phases. These can be listed by periods, as follows:

A. Period preceding burial of eggs
   (1) Predation on adult unspawned fish.
   (2) Death of adult unspawned fish through other causes, notably as a result of barriers or insufficient water.
   (3) Losses of eggs through retention in the body or failure of fertilization.

B. Period of incubation and alevinage
   (1) Erosion or scouring, that is, removal of gravel and contained eggs or alevins by flood, with resultant death by mechanical injury, exposure to predation or deposition in unsuitable situations.
   (2) Asphyxiation. Mortality caused by insufficient exchange of gases with the environment, due to unsuitability of the original location or to subsequent deposition of silt, etc., resulting in reduction of the water supply or reduction of the dissolved oxygen content of the water.
   (3) Unfavourable temperature for development.
   (4) Freezing of eggs or alevins by coincidence of prolonged cold weather with exposure of spawning beds to air.
   (5) Reduction of water level, resulting in death by desiccation or prevention of the emergence of fry from the gravel.
   (6) "Superimposition" or "overdigging". Mortality of the same type as in (1) but caused by the operations of fish which have occupied spawning sites already containing the developing eggs of earlier-spawning parents.
   (7) Killing of eggs or alevins by fungus.
   (8) Predation.
   (9) Exposure of eggs to salt water in tidal areas.

C. Free-swimming period
   (1) Predation.
   (2) Trapping of fry in pools or backwaters.

Presumably certain additional losses may occur in any of the above-mentioned phases through the action of disease or constitutional weaknesses. Little is known of the incidence and variability of such factors.

Breakdowns of total freshwater mortality by assigning percentage losses to such categories as the above have been made in specific instances by Hobbs (1937) for *Oncorhynchus tshawytscha* and *Salmo fario* and by Cameron (1941) for the present species. Two main difficulties are encountered in attempting to reach general conclusions as to the relative importance of such individual factors in determining the final output. The first lies in the absence of quantitative data indicating the variation which undoubtedly exists in different streams and different years. The second difficulty is connected with the fact that many of the factors recognized are interrelated in such a manner as to make the assignment of losses an arbitrary matter. For example, the losses among pre-spawning fish may be assigned largely to a biological factor, predation. The extent of this predation, however, may depend to a large extent on a non-biological factor, namely the prevailing water level. For example, the writer has observed rather heavy predation by bears on unspawned pink salmon which had been prevented from surmounting a waterfall by low water conditions: later, an increase in stream flow largely eliminated the losses at this spot. On the other hand, to isolate and emphasize such factors as scouring and silting as being the chief causes of mortality during the period between deposition and fry emergence may underem-

phasize the part played by biological factors in producing the result. The size of the run may determine the proportion of the fish which are forced to select less desirable sites. Again, a comparatively small difference in high water levels might greatly alter the ratio of losses between "silting" and "scouring" without producing a corresponding effect on the total mortality.

3. *General conclusions.* While mortality will be discussed further, on a different basis, on later pages, the foregoing brief review of the extent and nature of freshwater losses favours the following preliminary conclusions:

Freshwater mortality is always heavy, accounting for a large majority of the eggs or young fish present.

Large fluctuations in the output of fry per parent are caused not by major variations in the total mortality rate but by small variations which are large in relation to the very small percentage of fish which normally survive.

While considerable annual variations in percentage survival are evident in a given stream, there are also significant average differences in the mortality rates of populations inhabiting different streams.

Populations having a low average freshwater survival are likely to show large relative differences in efficiency of reproduction from year to year.

The immediate causes of death are interrelated. Specific factors are not necessarily additive in effect but act reciprocally to some extent. Total mortality may therefore be expected to vary relatively less than mortality from a particular cause.

MORTALITY AND SURVIVAL IN THE OCEAN

As indicated previously, the mortalities which take place in the ocean can conveniently be referred to two categories—natural mortality and fishing mortality.[2] Before attempting the segregation of these it is convenient to establish a basis for estimating their combined effect on the young fish which have escaped from fresh water.

The number of adult fish entering a given stream from the sea will represent numerically the survival of the young migrants leaving the stream in the appropriate previous season(s) *if* (*a*) all the survivors return to the parent stream, or (*b*) the number of survivors which do not return to the same stream is balanced by an equal number of fish which originated elsewhere.

With regard to (*a*), reference may be made to marking experiments reported by Pritchard (1939). This investigator found that in the year for which the most reliable data were available, 90 per cent of the recoveries were from the "home" stream and only 0.2 per cent were recovered in areas and at times which appeared to preclude their return to McClinton Creek. He concluded on the basis of all the evidence "that some of the pink salmon in the natural run may wander from the parent stream but the numbers so doing are not economically significant". Also, "For all the marking experiments on pink salmon it can be stated that in

[2]In the largest rivers, namely the Fraser and the Skeena, some commercial fishing takes place in fresh water. Since, however, this fishing is a direct continuation of operations which for the most part are prosecuted in the sea, the distinction is not recognized in the present account.

the case of natural runs the majority of fish returned to the parent stream". In a later paper Pritchard (1948b) supported his conclusion by reporting the results of an examination of pink salmon carcases in streams other than the parent creek. He found only two marked fish in 5,922 examined, whereas McClinton Creek showed a proportion of marked fish equivalent to 131 in 5,922.

(*b*) Even with respect to the small minority of fish which undoubtedly "wander", it may be presumed that such wandering is not in one direction only but that there is a tendency for absentee fish to be replaced by individuals which originated in other streams.

It is therefore concluded that the escapement of adults to a stream usually represents very closely the numerical survival from that stream's output of young fish.

In the instances for which data are available, the percentages of returning adults in relation to outgoing fry are given in Table IV.

TABLE IV. Marine survival of pink salmon. Adult escapement to fresh water expressed as percentage of outgoing fry.

Locality	Brood year	Number of experiments	Range (%)	Geometric mean (%)	Authority
McClinton Creek	1930–40	6	0.29–6.75	0.824	Pritchard (1948)
Morrison Creek	1943	1	....	2.10	Neave (unpublished)
Hooknose Creek	1947–48	3	3.1–5.2	3.74	Hunter (1951)
Sashin Creek	1940–45	6	0.6–3.5	1.61	U.S. Fish & Wildlife Service*

*The writer is indebted to M. G. Hanavan, Acting Chief, Alaska Fishery Investigations, for these figures which are of great interest for comparative purposes.

These survival figures represent the adult population after it has been subjected to both natural ocean mortality and fishing mortality. For practical purposes these two factors can be considered to operate consecutively, not concurrently. The fishing for this species takes place during such a relatively short period at the end of the ocean phase that natural ocean mortality can be regarded as having ceased when fishing mortality begins. Fishing mortality therefore does not reduce natural ocean mortality to a significant extent, but is added to it.

So far, it has not proved feasible to separate natural mortality from fishing mortality in the case of individual streams. The reasons are mainly connected with (*a*) the difficulty of obtaining a complete, or reasonably complete, recovery of marked fish from a fishery which is prosecuted to a large extent with purse seines and which delivers catches at widely separated points; (*b*) uncertainty about the relative effects of natural and fishing mortality on marked and unmarked fish; and (*c*) the heavy differential mortality which is believed to follow the marking of fish which must be operated upon when only 30-40 mm. long.

It is possible, nevertheless, to reach certain general conclusions about the order of magnitude of the two types of mortality to which fish are subjected in the ocean.

The average survival represented by the final escapements (Table IV) is about 2 per cent. Evidently the survival from natural ocean mortality must be

sufficiently greater than 2 per cent to account for a fairly intensive fishery. At the same time we might expect that the average survival would be considerably less than the 9.9 per cent which Foerster (1936) estimated as the ocean survival for sockeye. Although the latter species commonly spends a year longer in salt water than the pink salmon, this factor, in the opinion of the writer, would by no means offset the vulnerability associated with the very small size at which pink salmon reach the sea.

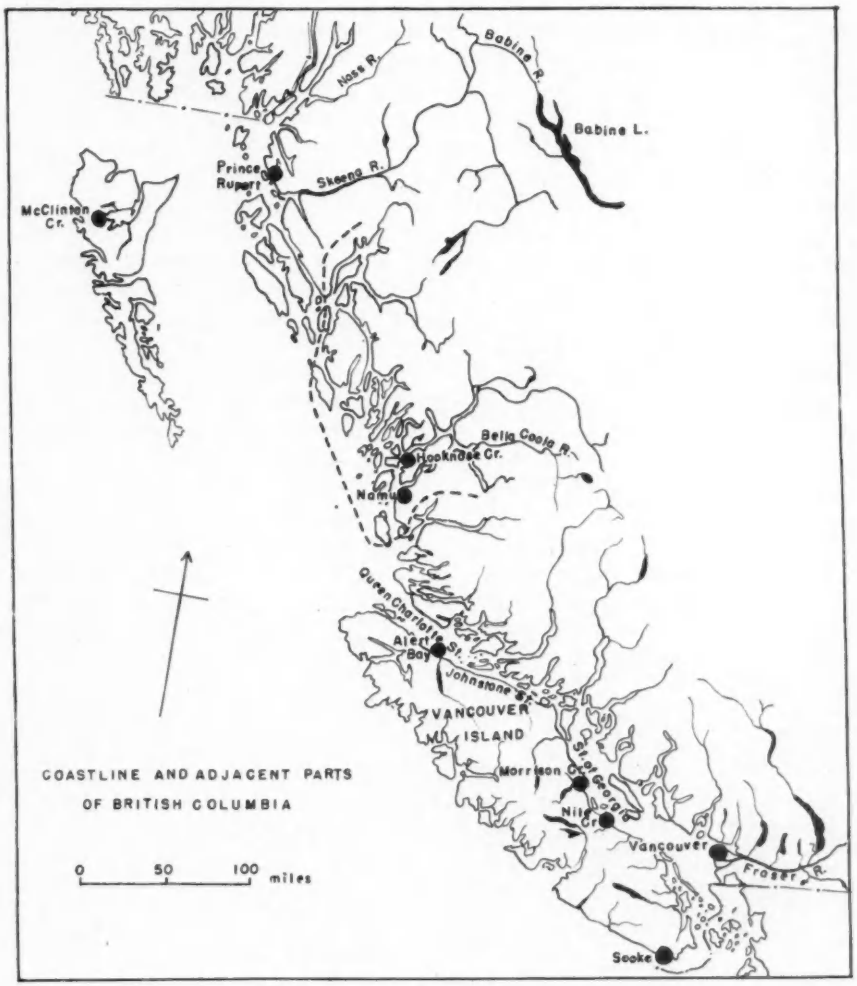

FIGURE 1. Portion of British Columbia, showing positions of localities referred to in text. Broken line delimits "central region" as this term is used in text.

The most obvious source of information on the point at issue is a comparison between the catches and escapements of certain areas. For such comparisons to be valid, the fish caught must be proceeding to the streams with the spawning populations of which they are being compared. In many areas there is no certainty whatever that the fish caught are related to the spawning streams of the same area. This is particularly true of the fish which enter the straits between Vancouver Island and the mainland and which tagging experiments show may be proceeding to any of a wide variety of localities from Queen Charlotte Strait to Puget Sound. There is, however, a large region of the central part of the British Columbia coastline, corresponding with the Department of Fisheries Statistical Areas 6, 7 and 8 (Figure 1), which can reasonably be considered as a self-contained unit in respect to catches and escapements. Taggings carried out under the direction of the writer at the south and north ends of this region in 1947 and 1948 showed little migration to other areas (only about 3 per cent of the tags recovered came from "outside" districts (unpublished data)). A comparison is accordingly presented (Table V and Figure 2) between catches and escapements reported for this region by officers of the Department of Fisheries. "Catches" were reported in hundredweights and have been converted to approximate equivalent numbers of individuals. The escapements quoted have been arrived at by summing the estimates of spawning populations made by inspectors on about 180 individual streams and rivers (I am indebted to Mr. J. G. Hunter for this compilation). Estimates have usually been recorded by observers by means of letters indicating that the population was within certain limits, for example "H" = between 5,000 and 10,000 fish. In order to obtain numerical totals the midpoints of the indicated ranges were assigned to the estimates.

TABLE V. Estimated catch and escapement of pink salmon in the central region of British Columbia.

Year	Catch	Escapement	Total run	Percentage caught
1934	2,250,000	2,046,675	4,296,675	52
1935	1,682,000	1,205,875	2,887,875	58
1936	3,502,000	2,577,500	6,079,500	58
1937	1,841,000	909,050	2,750,050	67
1938	1,619,000	1,512,425	3,131,425	52
1939	2,800,000	970,800	3,770,800	74
1940	663,000	622,875	1,285,875	52
1941	1,073,000	916,250	1,989,250	54
1942	1,175,000	1,045,600	2,220,600	53
1943	5,250,000	1,805,150	7,055,150	74
1944	2,510,000	856,400	3,366,400	74
1945	6,900,000	2,517,275	9,417,275	73
1946	1,685,000	724,775	2,409,775	70
1947	2,076,000	662,275	2,738,275	76
1948	2,834,000	985,100	3,835,100	74
1949	3,233,000	1,720,350	4,296,675	65

The difficulty of estimating accurately the salmon population of a stream on the basis of, at most, a very few visits during the spawning season is well known and fully admitted. Certain sources of error may be expected to cancel out when such a large number of observations is summed. In general, the catch seems to constitute a rather constant percentage of the run, whether the latter be large or small, although the degree of exploitation seems to have been maintained at a higher level since about 1943. Accepting this evidence of a rather constant relationship between catch and escapement,[3] we may defer acceptance of actual figures until another clue has been considered.

The taggings to which reference has been made yielded total returns from the fishery of about 30 per cent. In both instances tagging was carried out over a period of several weeks which, however, did not include the earliest stages of the fishing season. The recoveries of tags applied during the latter part of the fishing period will tend to be below the general fishing mortality rate (returns from the first week of tagging were 40 and 33 per cent respectively from the two operations). Even these figures are undoubtedly too low. Non-return of recaptured tags is believed to be a far from unimportant source of loss and even the earlier fish tagged had been available to the fishery for various lengths of time and represented a population which had undergone some depletion.

On the other hand, the fishing mortality deduced from the comparison of catch and escapement is probably somewhat high. Not all salmon streams are inspected in each year. A fraction of the escapement is thus unrecorded. The evaluation of runs in streams on which counting weirs are operated leads to the conclusion that stream patrol observations usually underestimate the populations which actually enter.

With these limitations in mind, the writer believes that the average fishing mortality in this region in recent years can be placed with some assurance at between 50 and 70 per cent of the adult run; 60 per cent would seem to be a reasonable working figure.

If we assume that the adult escapements of this large region approximate the general average found for various experimental streams, that is, about 2 per cent of the sea-going fry, this would imply an average survival of 5 per cent before the fishery takes its toll, or a natural ocean mortality of 95 per cent.

In certain other districts, fishing mortality may be greater. The size and mobility of the present day salmon fleet is such that a heavy fishery can quickly be brought to bear on a run of fish appearing in any section of the coastline. Pressure of fishing gear thus tends to be distributed according to the numbers of fish available anywhere. Certain runs, however, are undoubtedly vulnerable for a longer period than others, owing to their long migrations through confined straits and channels. Tag returns of 40 per cent were obtained from taggings carried out at Sooke and in the Alert Bay area in 1943 and 1945 (Pritchard and DeLacy, 1944; DeLacy and Neave, 1947). These figures imply a somewhat

[3]Such a relationship might well be expected, in view of the efficiency of the fishing fleet and the measures adopted by the Department of Fisheries to ensure the escape of a proportion of the run.

higher fishing mortality among salmon which travel to "inside" waters via Juan de Fuca and Johnstone Straits than among the fish of the central region.

While 5 per cent is considered to be an approximation to the average ocean survival prior to fishing, there is no good evidence as to the range of variation. In only one of the recorded cases (Table IV) does the return to a stream considerably exceed this figure (the 6.75 per cent observed in one year at McClinton Creek), indicating that natural survival must have reached this level even if fishing mortality was nil. The lowest recorded return (0.29 per cent) would imply a natural survival of less than 5 per cent unless the fishery took 94 per cent of the adult fish. This seems unlikely, although it is obvious that the average fishing mortality for a large district cannot be expected to hold good when applied to the run of a particular stream in a particular year. Further speculation on the limits of variation of natural ocean mortality would seem to be unwarranted until more data are available.

Changes in Abundance of Adult Pink Salmon

Figure 2, to which reference has already been made, may be cited as an example of changes in abundance when a large area is considered. Since the pink salmon has a constant life-span of two years, the "even"- and "odd"-year runs represent different stocks and can be treated separately in considering changes in population levels. Figure 3 shows the same data segregated into the two components.

Figures for the number of pink salmon caught annually in the traps situated near Sooke may be presumed to reflect with considerable accuracy the relative

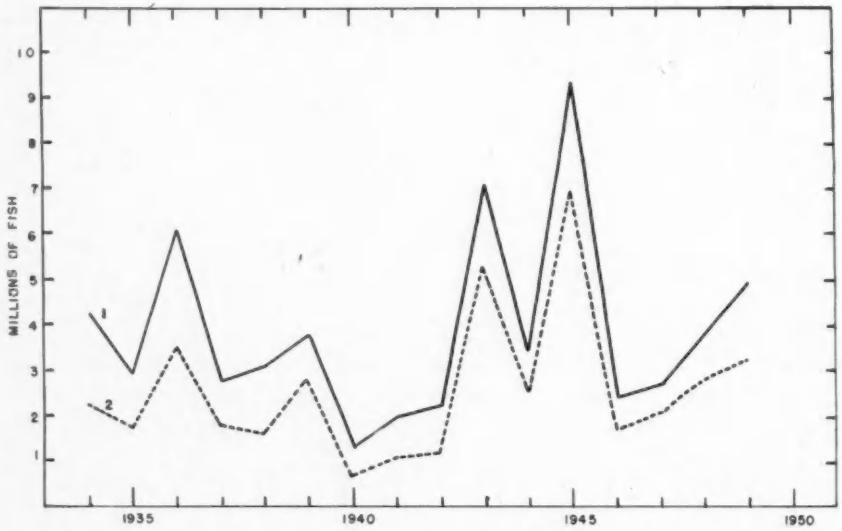

Figure 2. Reported catch and escapement of pink salmon in the central region of British Columbia. 1. Total run; 2. Catch.

magnitude of the runs entering Juan de Fuca Strait, since this gear is nearly constant in quantity and position from year to year and takes its toll at an early stage in the passage of the fish through the fishery as a whole. Since the difference in size between the "even"- and "odd"-year catches is so great as to make graphical representation inconvenient, the figures are tabulated (Table VI).

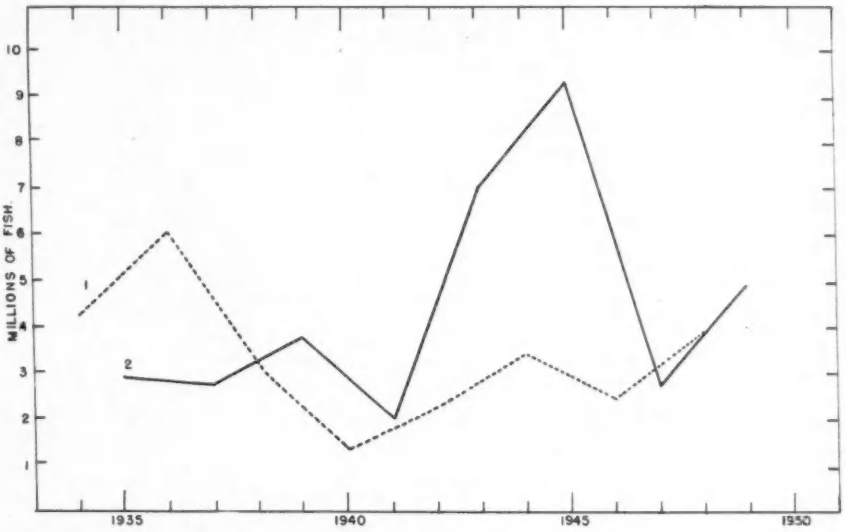

FIGURE 3. Reported runs of pink salmon in the central region of British Columbia. 1. Even years; 2. Odd years.

TABLE VI. Numbers of pink salmon caught annually in traps at Sooke, B.C.

Year	Number	Year	Number
1938	1,472	1939	169,018
1940	328	1941	55,503
1942	116	1943	33,699
1944	605	1945	221,871
1946	110	1947	168,284
1948	214	1949	109,304
Average	474	Average	126,280

The evidence (discussed previously) that the annual catch made by other types of gear is closely related to the size of the run, indicates that catch figures alone may serve as indices of relative abundance in certain areas. Figure 4 shows annual catches reported for the Skeena River area over a lengthy period.

From these examples, which apply to large areas and do not necessarily reflect the course of events in individual streams, the following inferences can be drawn:

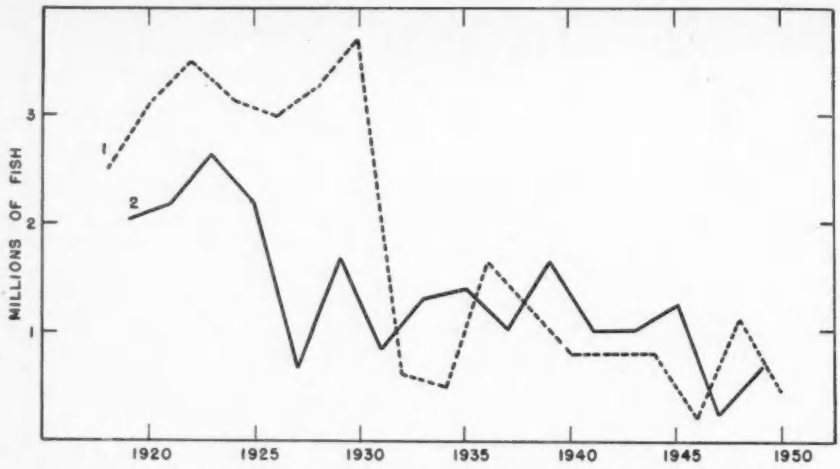

FIGURE 4. Pink salmon catches reported from Skeena River area. 1. Even years; 2. Odd years.

(1) Changes in abundance between one generation and the next do not usually exceed a two- or threefold increase or decrease (unless the numbers are very small, as in the "off" years of some areas). This is in spite of the fact that the rigid life-span of the pink salmon precludes any buffering effect which might be introduced if fish matured at different ages.

(2) Occasionally a larger "jump" or "crash" takes place, as is exemplified by the big difference between the 1930 and 1932 catches of the Skeena area. Actually this occurrence took place over a much larger area than that to which the graph refers, being a conspicuous feature of catch records for northern and central British Columbia.[4] A similar failure in the recurrence of the big "odd"-year run to the central region appears to have occurred in 1919. The sudden upswing of this stock in 1943 and the sharp recession in 1947 (Figure 3) are further examples of these discontinuous changes in abundance. An upward jump of similar relative magnitude is shown by the Sooke trap catches in 1945 (Table VI).

(3) After one of these major changes the population is apt to remain near the new level for at least a generation and sometimes for a prolonged period.

(4) The "even"- and "odd"-year stocks fluctuate independently, neither small nor large changes in one cycle being necessarily reflected by similar tendencies in the other cycle. The average level of abundance of the two cycles may be quite similar, as in the central region from 1934 to 1949 and in the Skeena area from 1931 to 1949, or the two stocks may exist for long periods on a totally different

[4]The possibility that the low catches of 1932 merely reflected economic conditions is discussed by Hoar (1951). The continued low level of the catches provided by this stock in the face of the high market demand of the last 15 years, together with the existence of a reasonable alternative explanation, seems to the writer to constitute convincing evidence that such a "crash" actually occurred. Moreover, chum salmon production, which should have been at least equally affected by economic conditions, showed a marked *increase* in this area in 1932 (see Figure 7).

scale, as demonstrated by the runs at Sooke, where the odd-year fish exceed the even-year fish in a ratio of more than 250 to 1.

The Mechanism Controlling Population Levels

In seeking to understand the above-mentioned features of population levels and population changes it is necessary to conceive a mechanism which will permit the occurrence of seemingly contradictory results. On the one hand we are confronted with the fact that the pink salmon has successfully withstood a heavy fishing mortality for many years. Since this fishery, if it had been merely added to existing mortality, would have wiped out the commercial importance of the species in a very few generations, it is evident that the reduction in the number of adult fish has been accompanied by an increase in the reproductive efficiency of the escapements. On the other hand, the evidence is equally plain that two stocks can exist for prolonged periods in the same area at very different densities, with no tendency to reach a common level. Furthermore, when a large stock suffers a major "crash" it may remain for many generations near the new level with no apparent tendency to regain its former numerical status unless or until some equally sudden "jump" takes place.

In considering this problem it is necessary to distinguish between three "types" of mortality, namely:

(1) Mortality which becomes relatively heavier as populations *increase* in density (and vice versa), thereby tending to stabilize the prevailing population level.

(2) Mortality which becomes relatively heavier as populations *decrease* in density, thereby tending to exaggerate fluctuations initiated by other causes.

(3) Mortality which is independent of population density, that is, taking a given percentage of the population, whatever the density of the latter may be.

Mortality of the first type has long been recognized as being the ecological basis on which the maintenance of intensive long-term fisheries depends. Its effect on stocks has been termed "resilience" by some authors (Thompson, 1944, 1950; Pritchard, 1948). For mortality which operates in this manner the term "density-dependent mortality" has been used in other fields, particularly in entomological studies (see Solomon, 1949). This accurately designates the relationship but seems cumbersome, particularly when it becomes necessary to recognize "inversely density-dependent mortality", that is, the type of mortality referred to in category (2) above. The present writer suggests *compensatory mortality* as a convenient term for the relationship now under discussion.

This kind of mortality appears to be highly characteristic of the period from spawning to the emergence of the fry. It might be supposed that physical factors such as flood, drouth and silting would tend to have the same effect on a population whether the latter be large or small. This is indeed the case to an important degree (see below) but these factors do not act in this way alone. In practice the spawning sites available in the limited environment of a stream appear to vary considerably in favourability. With increasing numbers of spawners a larger percentage of the fish are compelled to make their redds in marginal or unfavourable

positions. This condition, coupled with the increased "superimposition" and perhaps the mutual interference between individuals of a dense population, tend to produce a lower average efficiency of reproduction.

Over the whole period of freshwater existence Pritchard (1948a) at McClinton Creek observed a general inverse relationship between number of adults and percentage output of fry migrants. Certain anomalies were apparent, however, especially at the highest population level encountered. These are discussed below.

The importance of mortalities which become relatively *greater* with diminishing density of population (and vice versa) seems not to have been appreciated by fishery biologists. Quite evidently, however, there are influences which frequently prevent the effective operation of compensatory mortality, since otherwise the large and small populations of an area could not indefinitely preserve their respective numerical positions. There would be a constant tendency to converge. Such influences cannot be merely neutral. They must actively oppose the compensatory process, since the existence of the latter is beyond dispute. Actually, as we have seen, pink salmon populations can be relatively stabilized for considerable periods at a wide variety of levels. The anti-compensatory influences must accordingly act over a wide range of densities. The term *depensatory mortality* is proposed for the type of mortality which is inversely related to population density. The identification of the factors which work in this way, and the period in the life-history when they operate, are obviously matters of vital importance to our study of population changes.

A specific example of depensatory mortality appears to be provided by the observations of Davidson and Hutchinson (1943). These authors reported that in January 1942 a wholly exceptional flood caused extremely heavy losses among pink salmon eggs and alevins in the lower reaches of Sashin Creek. Surviving fry migrants came mainly from the upper reaches, an area which usually receives little seeding, being relatively rocky. Owing to the population pressure produced by an exceptionally large run of adults in the fall of 1941 an unusually large number of adult fish had utilized this upstream area.

Such occurrences are probably relatively infrequent and certainly cannot provide the constant counterbalance to the compensatory process which seems to be demanded by the observed maintenance of diverse population levels. Fishing undoubtedly *could* be prosecuted in a depensatory manner. The taking of a fixed quantity each year would mean that small runs would be heavily exploited and that large runs would be relatively lightly fished. But as we have seen the fishery does not seem to operate in this way at the present time, since closures are applied with a view to permitting the escapement of a relatively constant proportion of the run.

A form of depensatory mortality which seems more adequate to account for the observed facts is associated with the period of fry migration. This period, although short in duration, is a peculiar and critical phase in the life-cycle. It represents the precipitation of a large and very vulnerable population into the community of stream-dwelling organisms. The transience of the situation pre

cludes the establishment of any long-term balance between predators and prey. The migration is merely an exodus in which heavy losses are sustained without any significant compensatory growth or development on the part of the survivors.

In his study of the McClinton Creek fry run of 1941, Cameron (1941) tentatively estimated a 60 per cent overall mortality among fry passing to the ocean from a spawning area which extended for a distance of two miles from salt water (or a 32 per cent mortality based on the potential egg deposition). The mortality, however, varied with the distance which the fish had to traverse and also increased during the week by week progress of the run. He pointed out the probable advantages to the fry of an early, compact migration in reducing mortality during this period.[5]

General observations indicate that the predators mainly concerned with fry mortality are other fish, resident in the same stream or themselves migrating seaward at the time. In the localities investigated trout, coho smolts and sculpins are important. The small size of the fry and the nocturnal nature of their migration appear to prevent major inroads by terrestrial predators. Losses are therefore largely determined by the number and activity of the local aquatic predators. Even in years when production is relatively low, fry-migrants will ordinarily constitute a large and readily available food supply during the short period of their downstream migration. Hence (at fry-population levels above a certain minimum) the predators will tend to take a fixed number rather than a percentage and the mortality will be of the depensatory type. The total number of predators present from year to year will presumably vary less than the number of pink salmon fry, since several species are involved and various age-groups are represented.

TABLE VII. Effect of predation on the fry-migrant production of pink salmon at McClinton Creek

Year	Potential egg deposition	Fry migrants	Percentage efficiency	Hypothetical fry emergents	Percentage efficiency	Percentage predation.
1938–39	8,500,000	2,020,000	23.8	(9,610,000)	(110)	(86.2)
1932–33	13,200,000	2,300,000	17.4	9,890,000	75	57.6
1940–41	26,600,000	5,060,000	19.0	12,650,000	48	29.0
1930–31	50,800,000	5,384,000	10.6	12,974,000	25	14.4
1936–37	53,200,000	3,675,000	6.9	11,265,000	21	14.1
1934–35	139,500,000	12,600,000	9.0	20,190,000	14	5.0

The data provided by Pritchard and by Cameron for McClinton Creek may be re-examined in the light of this viewpoint. Cameron's estimated 60 per cent mortality represents 7,590,000 fry lost in 1941. Assuming predation to be constant from year to year, this figure may be added to each year's recorded fry-migrant output to obtain a theoretical figure for the number of fry escaping from the gravel. A comparison between Pritchard's figures for *migrant output* and these hypothetical figures for *fry emergence* is presented in Table VII.

[5]It is possible, although unverified, that earlier entrance into the sea might bring corresponding disadvantages if the seasonal increase of marine zooplankton were less advanced.

As might be anticipated, the calculated values for emergence produce an obvious absurdity at the lowest level of population, when the predators could hardly be expected to obtain the maximum number of fry which they are capable of devouring. In spite of the crudeness of the procedure, however, the adjustment produces a more logical relationship (inverse) between the size of the spawning population and the percentage efficiency of reproduction, every value now appearing in its proper sequence in the series. In particular, the anomaly of a higher percentage output from a deposition of 139,500,000 eggs than from one of 53,200,000 and the similar discrepancy between the efficiency at the 27,000,000 and 13,000,000 levels are eliminated. The reduction in the effectiveness of predation with increasing fry production is well illustrated in the last column of Table VII.

It may therefore be inferred that compensatory mortality prevailed over the whole size-range of the spawning populations observed at McClinton Creek *up to the time of emergence of the fry*. Subsequent predation, on the other hand, introduced depensatory effects which in some instances caused a transposition of the final results.

Recognition of these different kinds of mortality permits a reasonable explanation of the problems posed on a previous page. With other conditions constant, a reduction in the number of spawners (by fishing or other cause) will be followed by increased survival up to the free-swimming stage. The absolute number of fry produced may not be very different from the previous average (cf. the relative uniformity of "hypothetical fry emergents" from depositions of different magnitude) and fluctuations of the population will remain within moderate limits. If, on the other hand, the number of emergent fry is drastically reduced (as could happen through unusually unfavourable physical conditions or through the reduction of spawners below the level which could produce a large fry emergence even with the decreased mortality) the predators will take a larger relative toll and the population will be depressed to a new level. At the other extreme, a particularly abundant fry emergence may "break through" the control imposed by predators and enable the population to reach a level at which predation takes only a small percentage and control is effected mainly by compensatory mortality.

The depensatory part of the mechanism tends to resist a return to the former level. This would account for the apparent fact that pink salmon populations can become stabilized for long periods at very different levels and that new levels are sometimes reached by sudden "steps" rather than by gradual transitions. The term "level" is used of course in a comparative sense, to denote a period of relatively minor fluctuations. These, too, are presumably accentuated by predation but not to an extent which precludes rectification by ordinary climatic variations or other factors.

It is evidently the role of depensatory mortality to exaggerate changes and, by opposing compensatory mortality, to stabilize these changes when they become great. Since, however, neither compensatory nor depensatory influences can

initiate changes we must recognize the existence of a third type of mortality which is independent of population density. In conformity with the other terms suggested herein, this may be called *extrapensatory mortality.*

As already pointed out, certain physical factors in the freshwater environment may act to some extent in a compensatory manner—that is, their effectiveness is determined by the density of the population. There can be no doubt, however, that numerically similar spawning runs can show great variation in efficiency of reproduction. Favourable and unfavourable conditions of stream flow and temperature can operate at all levels of population density. The general effects of stream flow are discussed by Neave and Wickett (1949). In this publication Wickett has also shown a significant degree of correlation between the July-August precipitation and the number of adult pink salmon returning in the next generation in the central region of British Columbia.

Fishing mortality (at least as applied at the present time in the central region) is also extrapensatory in that it operates with nearly equal intensity on large and small runs. Since, however, it appears to take an approximately constant percentage every year, it merely conforms to population sizes which have been determined previously and cannot be regarded as a potent source of year to year fluctuations. A sufficiently intensive fishery could undoubtedly produce a declining trend, or a drop to a new level, by drastically reducing the number of spawning fish.

On the other hand, natural ocean conditions could act in a manner similar to the freshwater conditions mentioned above—for example, temperature and the quantity or availability of food supplies could produce variations which are unrelated to the size of the population. Further reference to this point is made in the following section.

Relative Effects of Freshwater, Natural Ocean and Fishing Mortality in Determining Population Levels

Although a large majority of the total losses attending the life-cycle takes place in fresh water, it does not follow from this fact alone that fluctuations in population size are determined in this medium. Variation in mortality, rather than its total magnitude, will be important in this connection. Actually, since the individuals (or potential individuals) entering either environment commonly suffer a mortality exceeding 90 per cent before concluding the phase, it is evident that a small change in mortality rate in either instance would exert a profound effect on the end result.

Pritchard (1950) found that at McClinton Creek the *total* ocean survival (adult escapement/fry entering the sea) showed greater relative variation (that is, ratio between highest and lowest recorded values) than the freshwater survival (freshwater survival, 23.8 to 6.9 per cent, ratio 3.5:1; ocean survival 6.75 to 0.29 per cent, ratio 23:1). There are reasons, however, for believing that this is not a representative comparison between the variability of freshwater and *natural* ocean survival. Corresponding figures for other localities are:

	Percentage freshwater survival	Freshwater ratio	Percentage ocean survival	Ocean ratio
Sashin Creek	6.4 – 0.2	32:1	3.87 – 0.74	5.2:1
Hooknose Creek	15.0 – 0.87	17:1	5.2 – 3.1	1.7:1

The combination of McClinton Creek data with these other records gives a total freshwater ratio of 119:1, without extending the McClinton Creek range for ocean variability.

The small degree of variation in the freshwater survival at McClinton Creek is evidently due to the absence of such low values as have been found elsewhere. The relative stability of the stream conditions at McClinton Creek during the period of the investigations is attested by the good relationship (already discussed) betwen the size of the spawning population and the efficiency of fry production. Evidently no drastic extrapensatory factors intervened to upset this relationship. Under such circumstances it is quite possible that changes in population size can be determined in large measure by natural ocean conditions. However, it should be noted that the figures given are the net result of natural *and* fishing mortality. Although we have found reason to believe that fishing mortality takes a relatively constant percentage from year to year when a large area is considered, such constancy cannot be expected to prevail for the run to an individual small stream. Pritchard himself considered that the intensity with which the McClinton Creek run was fished varied a good deal. The low ocean survival observed in most years at McClinton Creek, contrasted with a very high survival in one year, suggests the possibility that this run is usually fished heavily but can on occasion escape major exploitation.

As regards *natural* mortality, the present writer thinks that major importance in determining changes in population size can usually be assigned to freshwater factors, in view of the following considerations:

(1) On general grounds, physical conditions such as water volume, temperature and available space are more variable in fresh water than in the ocean. Moreover, the eggs or alevins, unlike the ocean fish, are unable to seek optimum conditions but must experience the full impact of environmental changes.

(2) According to the view expressed on previous pages, variations in fry production imposed by such changes are reinforced by the depensatory effect of predation on the outgoing fry.

(3) The apparent independence of even- and odd-year stocks in respect to fluctuations suggests that these originate in fresh water, which is the only phase in which these two populations are completely separated.

(4) A significant correlation has been found between a meteorological factor affecting spawning conditions and variations in the sizes of resulting runs.

(5) The output of fry migrants from fresh water is at times so low that a reduction in the adult population must necessarily result unless ocean survival is raised to a level which seems unreasonable in the light of existing information (see Figure 5).

(6) At each of the localities for which several years' data are available (McClinton Creek, Sashin Creek, Hooknose Creek) there appears to be a relation between the efficiency of freshwater reproduction and the direction of size change in the resulting adult escapement. The most striking instance has been the change

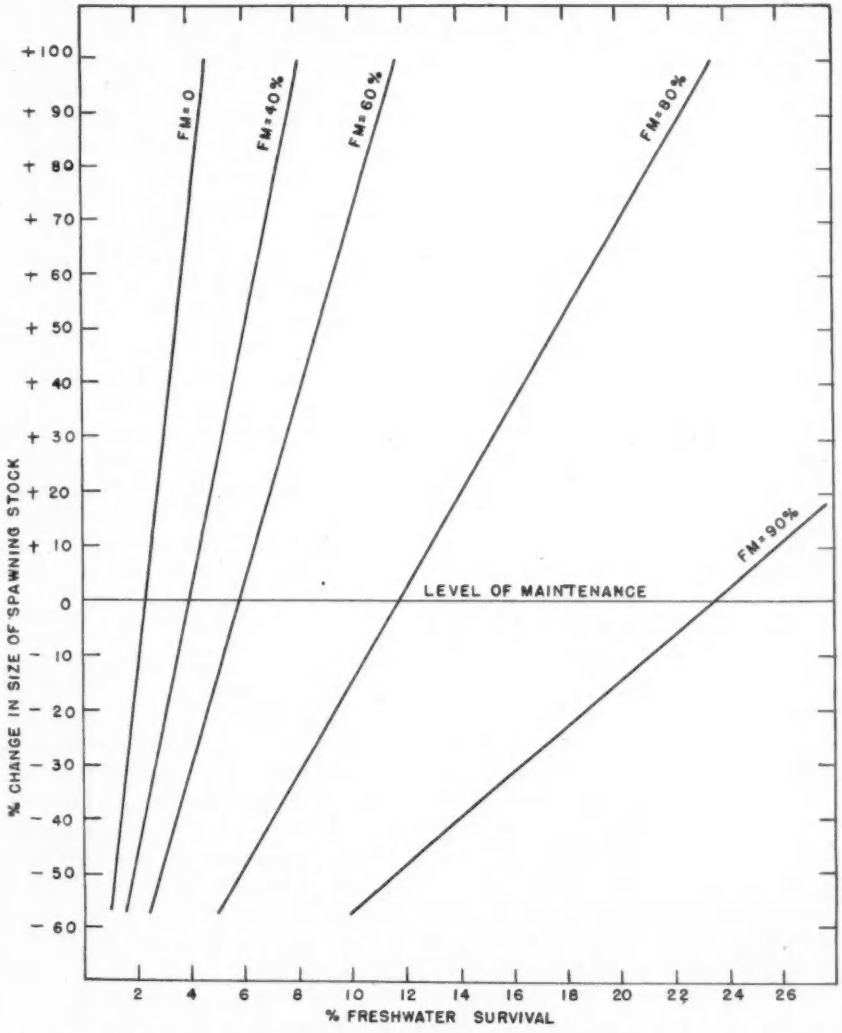

FIGURE 5. Relation between freshwater survival of pink salmon and size of spawning stock at various levels of fishing intensity. An average natural ocean survival of 5 per cent is assumed. F.M., fishing mortality.

from a larger odd-year run to a larger even-year run, observed at Hooknose Creek. Here, an adult escapement of 5,576 fish in 1947 produced only 33,000 fry-migrants entering the sea. The adult return in 1949 was 1,173 fish. The 1948 escapement of 1,160 adults produced an output of 64,000 migrants, resulting in a return of 1,857 mature fish. It seems clear that the change in relative size of the two stocks was initiated in fresh water.

In only one important respect does ocean life seem to offer opportunity for greater variability in natural mortality than does freshwater existence. This is in the availability of food supplies, a problem which is of relatively small importance in fresh water. The appreciable differences in average size of individual pink salmon in different years (see Hoar, 1951) are probably due, in part at least, to feeding conditions. This factor may well be responsible also for variations in mortality. The role of marine conditions in determining population size cannot be dismissed as insignificant, although the writer believes that their effects are usually much smaller than those of freshwater factors.

A question of some interest and importance is whether or not ocean mortality tends to be compensatory—that is, whether it tends to offset the numerical variations in the fry populations which enter the sea from year to year. Any such tendency would of course limit the effectiveness of remedial measures based on increasing the output of sea-going migrants. If the reasons already advanced for considering freshwater factors to be largely responsible for determining fluctuations are valid, then compensatory influences in the sea, if they exist, must be small, since on average they do not obscure the effects attributed to fresh water. Davidson and Vaughan (1941) have, however, hypothesized the existence of intraspecific competition in the sea as a factor affecting the average *size* of individual pink salmon of the Clarence Strait area of southeastern Alaska. This view was based on an inverse relationship between size of populations and size of individuals of the adult runs.

It can be maintained on general grounds that pink salmon, however numerous, constitute but a small element in the complex economy of the sea. It cannot be supposed that there is a special limited and relatively constant food supply exploited only by pink salmon. If other species are involved (for example herring, chum salmon and the various other vertebrates and invertebrates which feed on the same kinds of zooplankton) the degree of competition should be determined by the total population of this association of species, not merely by the fluctuating abundance of pink salmon. The effects would also be distributed. In other words, the rather moderate changes in pink salmon abundance reported by Davidson and Vaughan would have to alter the relation between the available food supply and all the animals using it before specific effects on pink salmon became apparent. Ordinarily, the chances that such an interaction would be detectable in the face of annual changes in food availability wrought by such factors as water temperature, amount of sunlight or prevailing wind, would seem to be small. Perhaps a degree of such competition may occur in areas where the output of young pinks is very high and the fish tend to remain within restricted ocean areas. On the British Columbia coast Hoar (1951) found no inverse asso-

ciation between body size and population size. He noted, however, that changes in body size are in the same direction over the whole British Columbia coast and that odd-year fish tend to be larger than even-year fish, in spite of the fact that in some districts they are far more abundant. Since the even- and odd-year stocks are effectively segregated as regards interbreeding, the possibility of a genetic factor may be entertained.

The idea of compensatory *size* adjustment is more or less opposed to compensatory *mortality*. The occurrence of the latter would, naturally, tend to eliminate the differences in abundance with which Davidson and Vaughan associated large and small fish. As mentioned, the evidence at present available indicates that on the British Columbia coast neither the mortality of a year-class nor the individual size of its members is determined to an appreciable degree by its own abundance in the ocean. Perhaps the most convincing argument against the general occurrence of compensatory mortality in the sea is to be found in the persistent disparity in the numbers of even- and odd-year stocks which has already been mentioned as characteristic of certain areas. A mechanism for establishing and maintaining this disparity has been suggested on previous pages. Such a condition could not be maintained, however, if ocean mortality tended to favour small populations and reduce large ones.

The views presented above have received support from a recent study by Murphy and Shapovalov (1951). These authors, referring to king salmon (*O. tshawytscha*), silver salmon (*O. kisutch*) and steelheal trout (*Salmo gairdnerii*) on the California coast, present evidence which "suggests the absence of any general, widespread density-dependent factors operating upon these fish in the ocean along the Pacific Coast at the present levels of population abundance. It may also be inferred that variation in density-*independent* coastwise factors in the ocean is slight from year to year".

By accepting the view that freshwater and ocean mortality vary independently and that fishing mortality tends to remove a fairly constant percentage, certain effects of varying these elements can be noted. The calculations presented represent *averages* which might be expected to prevail over a period long enough to eliminate the effects of annual fluctuations. Figure 5 shows the effect on the spawning stock of various rates of fishing intensity and freshwater survival, on the basis of an average egg-production of 1,700 eggs per female and a natural ocean survival of 5 per cent, which has been considered to represent an approximate average for this phase. A 50-50 sex ratio is assumed. The percentage freshwater survival required to keep the population constant at various levels of fishing intensity is indicated by the "level of maintenance".

It can be seen that under the postulated conditions the average freshwater survival of an unfished population must be quite low (2.35 per cent) if the population is not to keep on increasing. The addition of a 40 per cent fishery would require an increase of 67 per cent (that is, to about 4 per cent) in freshwater survival. A freshwater survival of approximately 6 per cent (that is about 150 per cent greater than the survival indicated for an unfished population) would permit a fishing mortality of 60 per cent. This is approximately the condition

(both of freshwater survival and fishing intensity) which is indicated by the data at present available for the central region, if Hooknose Creek figures can be taken as a guide. Figure 5 shows the great increase in reproductive efficiency which is required to offset still higher levels of exploitation. Whereas a rise in fishing intensity from 40 to 60 per cent demands an increase of 33 per cent in freshwater survival, a rise from 40 to 80 per cent would demand a 200 per cent improvement in the efficiency of fry output. Although compensation on this scale seems startling it has possibly been accomplished at McClinton Creek. The high average freshwater survival (mean = 13.15 per cent) is accompanied by a low return of adults and it would be unnecessary to revise our working figure of 5 per cent natural ocean survival if fishing mortality amounted to 80 or 85 per cent. Such a fishing intensity would not be out of line with the known exploitation of Fraser River sockeye runs and could perhaps be readily achieved where large populations are funnelled into a restricted area such as Masset Inlet. It may well be, of course, that average ocean survival varies in different areas. If the marine habitat of McClinton Creek fish is less favourable than that of central region fish, it is not necessary to assume such a high fishing mortality.

Obviously, however, the ability of a population to sustain a fishery will depend upon the extent to which compensation is possible. With increasing exploitation a premium will be placed on stocks which reproduce under such favourable external conditions that, in the absence of a fishery, their continual increase is largely prevented by factors associated with their own density. The prevalence of compensatory mortality over a wide range of population levels has been indicated at McClinton Creek, and under such conditions a high rate of exploitation is possible.

It may be confidently expected, however, that in many streams the efficiency of fry output is determined to a much greater extent by extrapensatory or depensatory factors. The physical conditions may be so rigorous or so variable that differences in population size do not produce corresponding changes in reproductive efficiency. Under some conditions a small population may be nearly as vulnerable to flood or drouth as a large population, in addition to suffering relatively heavier losses through predation. The imposition of even a moderate fishery on such a stock will produce a decline, whatever the total initial size of the population may be.

At the risk of repeating an obvious proposition, it may be emphasized that the effect of a fishery is to reduce *the mortality which is directly related to population density*. As we have seen, much of the mortality which attends the life-cycle is not of this nature and will be unaffected or even actually increased by a fishery. We have also expressed our belief that the compensatory potentialities are wholly or mainly located in that part of the life-cycle which occurs between spawning and the emergence of the fry from the gravel. On this view, the average maximum fishery which a stock can sustain (in the absence of artificial control) is determined by the degree of adjustability of the mortality during this relatively short period—which also happens to be a period when another type of mortality (extrapensatory) may produce important effects.

The left-hand side of the following tabulation gives a generalized representation of the manner in which we might expect mortality to be distributed in the progeny of a pair of fish belonging to a stable, unfished population.

	Unfished	60 per cent fishery
Parents	2	2
Eggs	1,700	1,700
Emerging fry	100	250
Fry entering sea	40	100
Mature fish	2	5
Escapement	2	2

To provide a stable population at the 60 per cent fishing level the distribution of mortality must be altered in some such manner as is suggested in the right-hand column. This scheme applies only to the offspring of individual pairs of fish and leaves out of account the total size of the population. If compensatory influences are so strong that after subtraction of 60 per cent of the adult population the remaining 40 per cent can produce the same total number of fry (that is, the required increase in reproductive efficiency per pair of fish can be realized immediately), then the average size of adult *runs* should not decline, in spite of the reduced escapement. If, on the other hand, the reduced escapement cannot make good the losses caused by fishing there will be a tendency for the population to fall until a level is reached at which the individual pairs of fish can attain the required reproductive efficiency. Probably some adjustment along these general lines can frequently be made. However, a marked lowering of the total fry population, as we have seen, is attended by the danger that predation will become relatively more intensive, so that increased percentage survival up to the time of emergence is offset by reduced survival of migrating fry.[6] There seems to be no inherent reason why a crash should not be prolonged into a further decline (that is, a stabilized level might not be reached in one generation), but under the mechanism envisaged the initial drop is likely to be sudden and severe. Similarly the building up of a population might continue after a sharp rise. Some evidence of this can perhaps be seen in the Skeena and central region graphs. The further increases could, however, merely represent seasonal deviations from an established "level".

Conservation Problems

In spite of the indicated possibility of continued declines, the writer sees no convincing evidence of gradual long-term decreases in the existing populations, when large areas are considered. Reference has already been made to the occurrence of jumps or crashes, followed by the establishment of a new level. A "trend-line" covering a period in which such a "step" has occurred will of course slope upward or downward but such a line may give a false impression of gradual change. As indicated previously, the current "decline" of the Skeena and Nass

[6]Suppressive effects of this kind might of course be less pronounced if certain predators (for example coho, trout) were themselves declining at the same time.

areas appears in the main to represent a change in level which appeared in the odd-year stock in 1927 and in the even-year stock in 1932. There is some indication that a further drop in the odd-year stock may have taken place in the 1945-47 cycle (Figure 4).

A general association between fluctuations in abundance and physical conditions in fresh water has been indicated. There is evidence that crashes are the result of the same factors operating with exceptional severity, although it is not always possible to be dogmatic about the specific causes of events which happened many years ago. Very low water levels were faced by the parents of the 1932 fish when entering streams in northern and central British Columbia in 1930. The August rainfall in these districts was about 76 per cent below the mean (Dept. Marine & Fish., 1932). In 1945 there was an August rainfall deficiency of similar magnitude, with September precipitation also well below normal. The abrupt drop in population size from 1945 to 1947 affected not only the Skeena fish, which were already at a relatively low level, but also the central region fish, which were at a peak of abundance in 1945 (Figure 3). In 1925, climatic conditions in the Skeena area at spawning time do not appear to have been unfavourable but an extremely heavy precipitation which occurred in the lower Skeena valley in February 1926, accompanied by unseasonably high temperatures, may well have produced a destructive flood. The failure of the pink salmon run of the central region in 1919 followed wholly exceptional floods in that region in the autumn of 1917.

Sudden failures can thus be logically attributed primarily to physical conditions experienced in fresh water. There remains, however, the possibility that intensive fishing may keep spawning populations down to a level at which they are more susceptible to natural disasters. It may also tend to prevent a low population from reaching the numerical strength necessary to "break through" and achieve a higher general status.

While it is beyond the scope of this paper to deal with specific cases and treatments, certain general conclusions or opinions are implicit in the foregoing discussions which might influence the approach to conservational problems and can be expressed briefly as follows:

Freshwater and natural ocean survival are largely independent of each other. Therefore improved output of migrants from fresh water will on average be reflected in larger runs of adult fish.

Under intermediate conditions of fishing intensity (60 per cent mortality) a total freshwater survival of less than 5 per cent is likely to produce a reduction in size of the spawning population. A freshwater survival of 2 per cent or less will on average reduce the population, even if no fishing takes place.

Large runs in both even and odd years are not fundamentally incompatible (many streams in the central region have heavy runs of adults in both cycles).

The general objective of remedial measures should be to change natural mortality into fishing mortality, while keeping total mortality (on a percentage basis) constant. In effect, this entails the promotion of the most favourable physical conditions for spawning, incubation and alevinage. In the absence of lethal

factors which are density-independent, compensation can exert its full effect in making good the loses inflicted by the fishery. At the same time, remedial measures should aim at producing a large *total emergence* of fry (not merely a high efficiency of individual reproduction), since a large fry population will suffer relatively less predation than a small population. A stock should be large enough to produce a maximal emergence even at the risk of some loss of individual efficiency.

From the point of view of conserving pink salmon alone, it may sometimes be better (and less costly) to ameliorate physical conditions merely at the places and times at which incubation takes place, rather than to effect general and permanent stream improvements which may have the effect of also raising the stocks of predators. In other words, since nursery grounds and feeding areas are not required for the present species, control of water supply might be limited to an area sufficient to accommodate the eggs.

Predation is believed to be a major factor in keeping stocks at a low level. The elimination of predators (or the protection of fry from their attacks) should greatly increase the contribution to the fishery of stocks which are in this condition and should tend to prevent further drops. The effect on stocks which are at a high level of abundance would be much less pronounced. It may be argued, however, that certain predators (for example coho, trout) are more valuable than pink salmon.

The persistence of a low level of abundance (in the absence of a marked change in the condition or accessibility of spawning grounds) means that the total fry emergence is not large enough to escape excessive depensatory mortality, in spite of the increased reproductive efficiency of individual fish. The spawning stock should therefore be increased to the greatest possible extent, even if no current "decline" is evident. In thus attempting to establish a higher level, a brief total closure of the fishery would seem to be sounder conservational practice than the institution of a reduced fishing rate over a longer period. While even a total escapement of the adult run might not suffice to make the "jump", it would offer a chance of success, especially if it happened to coincide with favourable climatic conditions. A successful result would enable fishing to be resumed at the former percentage level but on a much larger stock. It could be expected that the new high population level would be terminated after a longer or shorter period by a major drouth, flood or other unfavourable circumstance. Such events seem to be of infrequent but irregular occurrence. The advent of a particularly severe season shortly after the establishment of an enlarged population would not necessarily nullify the advantage of increasing the stock, since the latter might be prevented from sinking to such a low level as would otherwise be reached. Ideally, the provision of an increased escapement would be accompanied by protection of the freshwater stages from the indicated adversities.

The maximum sustained fishery which can be imposed on the existing runs of different streams varies widely (not improbably from 80 per cent to zero), hence an escapement which is adequate for a particular area should not be presumed to be equally appropriate elsewhere.

In general, light runs should be little fished, in view of the danger that the cycle will be pushed to a persisting low level. The operation of the present protective measures, which tend to promote equal proportional pressure on large and small runs, is however definitely preferable to an attempt to pack the same quantity of fish each year. Such an attempt would defeat its own ends by reinforcing the depensatory processes which tend to exaggerate large and small runs.

In attempting to establish a run in a new locality or in a cycle which is not represented by existing populations, a satisfactory result would be unlikely unless (*a*) predators are not numerous or (*b*) the number of eggs or fry introduced is great enough to be equivalent to the product of a large natural escapement.

II. CHUM SALMON
Oncorhynchus keta (Walbaum)

The chum salmon is as widely distributed as the preceding species in the coastal waters of British Columbia and is common in certain streams, notably in the Vancouver Island district, from which the pink salmon is virtually absent. In some years it provides a larger catch, by weight, than any other species of Pacific salmon.

In certain glacier-fed streams of central and northern British Columbia in which a good flow of relatively cold water is maintained during the summer, some chums spawn as early as August 1st. Usually, however, the main runs enter fresh water somewhat later than the pink salmon, the most intensive spawning taking place between the end of September and mid-November. In some streams even later runs also occur, with fish still arriving in late December and January. In small coastal streams spawning usually takes place within a few days after entering fresh water. Although an occasional chum salmon reaches the upper Babine River, the species shows less inclination or ability than pink salmon to surmount obstacles and travel for long distances up streams. Much spawning

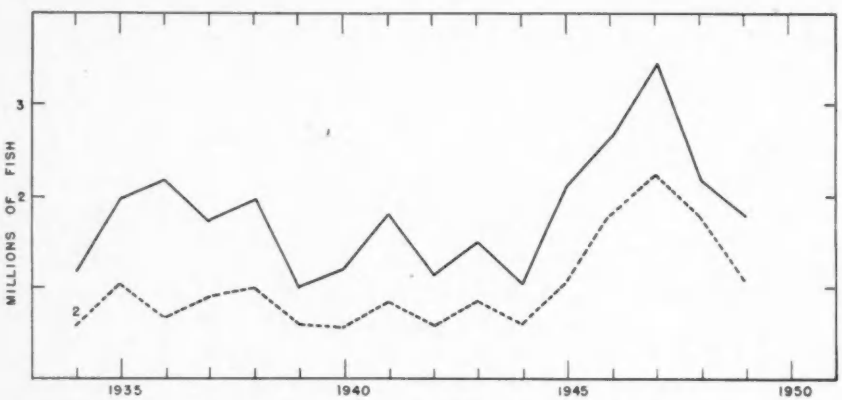

FIGURE 6. Reported catch and escapement of chum salmon in the central region of British Columbia. 1. Total run; 2. Catch.

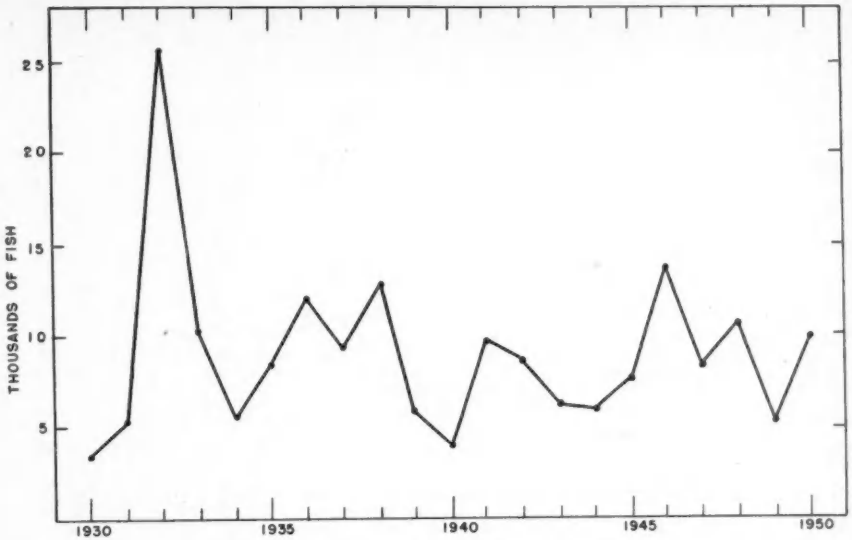

FIGURE 7. Reported catch of chum salmon in Skeena River area.

takes place very close to salt water. In conformity with the spawning habits the downstream migration of fry may extend over a somewhat longer period than that of pink salmon and the peak of this run is frequently reached about the middle of May. The habits of the young fish in salt water, so far as these have been observed, are similar to those of pink salmon, the two species being frequently found in company.

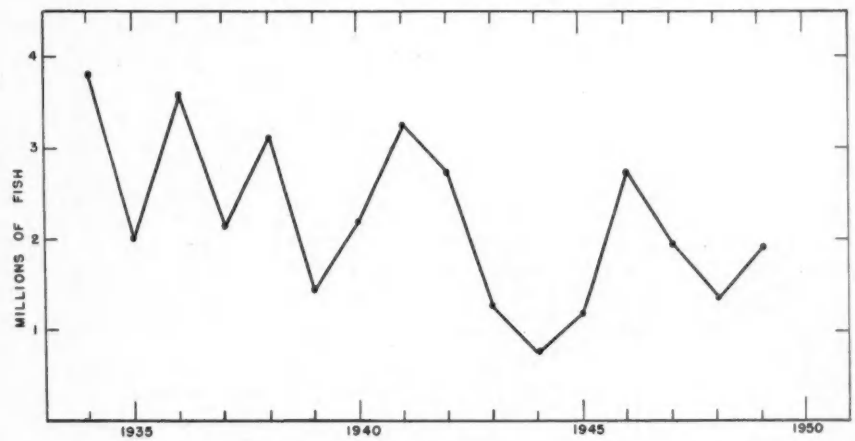

FIGURE 8. Reported escapement of chum salmon in Vancouver Island region.

The length of the life-cycle varies. While a majority of mature fish are usually four years of age, three-year-old and five-year-old fish are commonly represented. In commercial catches third-year fish occasionally constitute nearly or quite 50 per cent of local catches.

Since the problems and factors relating to the population sizes and changes of chum salmon are in many respects similar to those which have been discussed in connection with pink salmon, they will be presented here in the form of a comparison with the latter species.

Egg-Production

Egg counts for chum salmon in British Columbia have been reported as in Table VIII.

Table VIII. Number of eggs in female chum salmon.

Locality	Number of years	Number of fish	Average number of eggs	Authority
Namu	1	21	2,760	Foerster & Pritchard (1936)
Fraser River	1	51	2,943	" "
Nile Creek	3	47	2,726	Wickett (unpublished)
Hooknose Creek	4	114	2,254	Hunter (unpublished)
Average of all localities			2,671	

The general average of roughly 2,700 represents about 63 per cent higher numerical production than that of pink salmon. As already pointed out, this implies a different total mortality rate during the life-cycle. Otherwise, the abundance of the two species would diverge very rapidly.

Sex Ratio

The numbers of each sex recorded in spawning escapements to Nile Creek and Hooknose Creek are given in Table IX.

It will be seen that the deviations from equality are small and it seems fair to assume that a 50-50 ratio represents an average condition, as in the case of pink salmon.

Table IX. Sex ratio (per cent) of chum salmon escapements.

Locality	Years	Number of fish	Males	Females	Authority
Nile Creek	1945	3,062	49	51	Neave (1947)
	1946	1,861	51	49	Wickett (unpublished)
	1947	986	52	48	" "
	1948	386	54	46	" "
	1949	933	48	52	" "
Hooknose Creek	1947	10,106	48	52	Hunter (1948)
	1948	1,014	51	49	" (1949)
	1949	705	51	49	" (unpublished)
	1950	2,362	50	50	" "

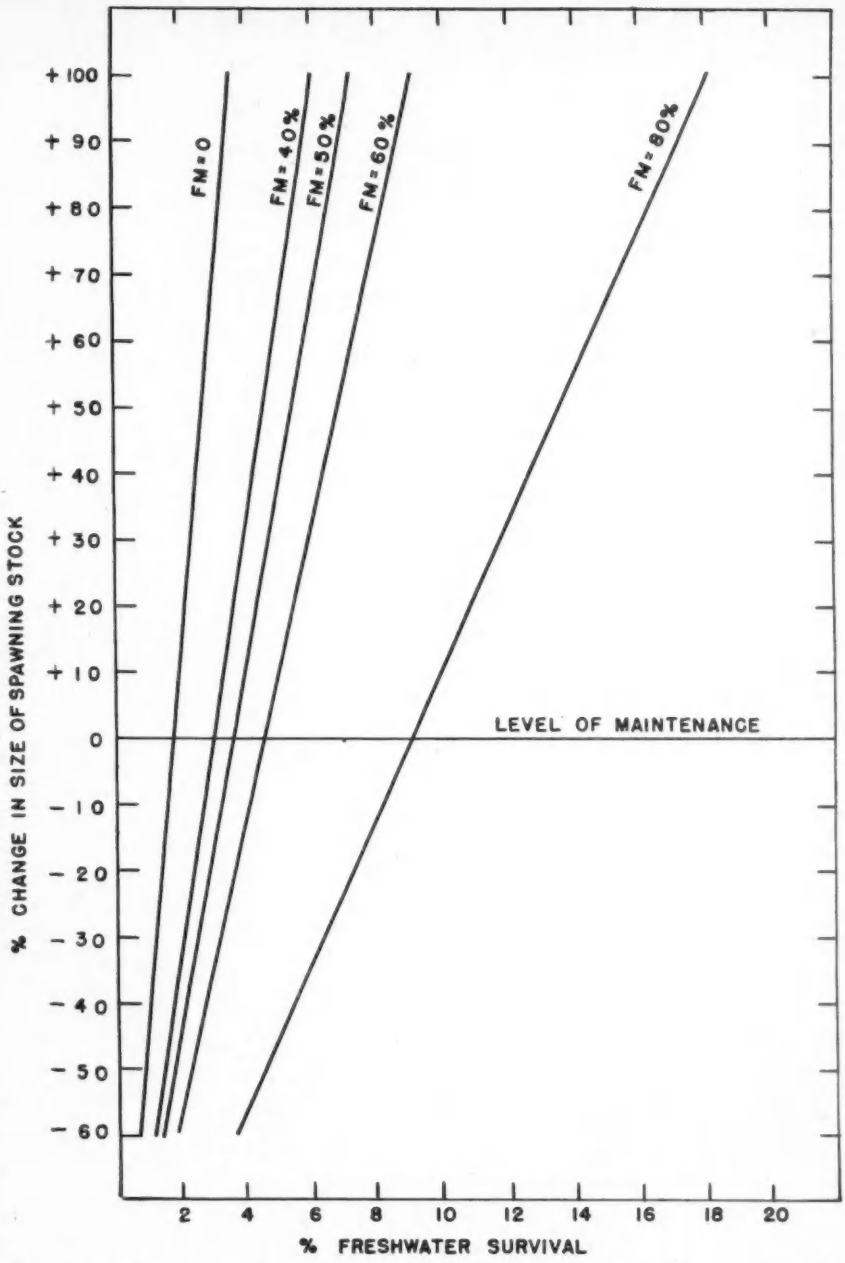

FIGURE 9. Relation between freshwater survival of chum salmon and size of spawning stock at various levels of fishing intensity. An average natural ocean survival of 4 per cent is assumed. F.M., fishing mortality.

MORTALITY

FRESHWATER MORTALITY AND SURVIVAL

1. *Total freshwater survival.* Quantitative records for the efficiency of reproduction during the freshwater phase in British Columbia are available only from Nile Creek since 1945 and Hooknose Creek since 1947. The estimated potential egg deposition and the recorded output of fry migrants at these two localities are given in Table X.

TABLE X. Freshwater survival of chum salmon.

Locality	Brood year	Potential deposition	Fry migrants	Survival (%)	Authority
Nile Creek	1945	3,540,000	138,388	3.90	Neave (1947)
	1946	2,115,000	8,319	0.40	Wickett (unpublished)
	1947	1,276,000	4,808	0.38	" "
	1948	385,000	23,188	6.03	" "
	1949	1,022,000	782	0.08	" "
Hooknose Creek	1947	10,977,000	108,746	0.99	Hunter (1948)
	1948	1,055,000	77,497	7.37	" (1949)
	1949	714,000	44,463	6.22	" (unpublished)
	1950	2,859,000	431,349	15.09	" "

The effect of the recorded outputs, in terms of the average number of fry migrants produced by a pair of spawning fish with a potential deposition of 2,700 eggs, would be as follows:

Stream	Observed mortality range	No. of migrants produced (*a*) Maximum	(*b*) Minimum	Ratio of (*a*) to (*b*)
Nile Creek	93.97 – 99.92	163	2.2	75:1
Hooknose Creek	84.80 – 99.01	410	27	15:1

While the ratio between highest and lowest recorded efficiency at Hooknose Creek is approximately the same as that of pink salmon in the same stream (see p. 455), much greater relative variation is evident at Nile Creek. At both localities, however, it is obvious that great variations in population size can be initiated in fresh water.

2. *Immediate causes of death.* All the specific causes of freshwater losses listed for pink salmon can be regarded as potential sources of mortality for the present species. The variability and interrelationship of these factors have already been emphasized but there appear to be certain quantitative differences in their effects on the two species although these differences cannot be measured accurately from existing data.

At the time when chum salmon enter fresh water the run-off in coastal streams has usually increased considerably from the low flows which prevail in August and September. Hence certain forms of mortality at this stage of the life-cycle are likely to be smaller than for pink salmon. The losses which may thus

be in varying degrees avoided might be more directly due to the impassability of falls; predation; exclusion from spawning areas by lack of water; unfavourably high temperature.

On the other hand, the less compact spawning run which frequently characterizes chum salmon increases the danger of superimposition by the later arrivals, which are frequently observed to select the same sites as earlier fish. Moreover, despite the larger number of eggs, chum salmon, owing to the much larger size of the fish and the space required for redds, probably cannot seed a limited area as efficiently as pink salmon. Overcrowding effects may thus appear at a lower population level, particularly since chums are apt to remain in the lower portions of spawning streams instead of distributing themselves throughout the accessible portions of the water system.

Many of the streams utilized by chum salmon show extreme seasonal or irregular changes in run-off. Losses due to erosion can therefore be severe. The very low percentage of fry migrants in certain years at Nile Creek appears to be associated with the incidence of floods in association with an unstable stream bed. Serious losses are also caused at times in Vancouver Island streams by the drying up of spawning beds in spring, thus preventing the emergence of fry, or by the trapping of the latter in pools before they can reach the sea (Neave, 1949).

3. *General conclusions.* In Hooknose Creek, where sizable runs of both species occur, the percentage efficiency of fry-migrant production has been almost identical for pinks and chums in each recorded year (Tables III, X). In this stream the two species utilize approximately the same areas and the spawning periods do not differ greatly in time. Ecologically they approach the status of a single population. However, the mere fact that both species have continued to maintain themselves in abundance in the same geographical areas, with no physical barriers against the effects of competition, indicates that in general pink and chum salmon occupy somewhat different ecological niches. In fact, one or other usually predominates in a given stream or portion of a river system and the situation at Hooknose Creek may represent an intermediate or overlapping condition between two such niches or habitats.

Very frequently chum salmon utilize streams which are quite unstable in respect to water flow and permanency of gravel beds, or in which large stones replace finer deposits. A rather extreme example is provided by Nile Creek. Factors which must give this species an advantage over pink salmon in offsetting these rigorous physical conditions are : (1) the greater egg-production, enabling the chum to withstand greater losses, on a percentage basis, (2) the larger size of the fish, enabling it to move larger stones and also to deposit its eggs at a deeper level, (3) the less rigid life-span, which prevents the effects of a "bad year's" reproduction from being entirely localized in a single recurrent cycle.

These advantages, which could account for the greater success of chums under adverse physical conditions, do not explain the failure of the species to oust pink salmon from the more favourable physical habitats of the latter. In this connection it may also be supposed that the balance of mortality due to superimposition would favour the later-spawning chum. The following suggestions,

however, can be offered. (1) As already pointed out, chum salmon do not distribute themselves as advantageously in relation to the potential spawning grounds and probably cannot seed utilized ground as thoroughly. (2) The later and more prolonged spawning season of the chum produces a later and less concentrated fry migration. This probably results in heavier losses to predators, which can be expected to be especially numerous in the relatively stable streams which are preferred by pink salmon.

In general support of these views on the different adaptations of the two species, certain population changes which appear to have taken place in some Vancouver Island streams may be cited. Following deforestation, which is presumed to have caused more extreme variation in stream flow, pink salmon populations declined to a very low level in such streams as Amor de Cosmos Creek, Oyster River and Nile Creek. At the same time chum salmon were able to maintain their numbers sufficiently well to become the dominant species in these waters.

It is concluded that, on average, production of fry migrants by chum salmon is somewhat less, on a percentage basis, than that of pink salmon and that it also tends to be more variable.

Mortality and Survival in the Ocean

Because of the longer life-span of chum salmon, data have not yet been accumulated which would furnish a guide to the percentage of outgoing fry from a given stream which eventually return to fresh water. However, if we accept 5 per cent as being a reasonable figure for the natural ocean survival of pink salmon, a simple calculation will suggest rather narrow limits within which the average chum survival should lie. On the basis of egg-production, total survival from egg to spawning adult (in stable populations) should be 17/27 times pink salmon survival. If the higher mortality of the chum takes place entirely in fresh water, the natural ocean survival should be the same in both species. If the difference lies wholly in the salt-water phase, the survival during this period should be $5 \times 17/27 = 3.15$ per cent. The possibility that chum salmon survival is much lower in one phase and somewhat higher in the other is difficult to entertain. We have already expressed the view that average freshwater survival is lower than for pink salmon. Marine survival would not be expected to be higher than for pinks, in view of the longer period for which the chum is exposed to ocean hazards. During a considerable part of their first summer, when the greatest marine mortality is presumed to occur, the two species have been observed feeding in company, and losses may be presumed to be of similar magnitude.

It is therefore suggested that average natural ocean survival for chum salmon in British Columbia is not less than 4 per cent.

Chum salmon fishing is prosecuted by the same methods as pink salmon fishing. The division between catches and escapements in the central region, based on information of the kind discussed on page 460, is shown in Table XI.

According to these figures the average catch constitutes a somewhat smaller proportion of the run than is the case with pink salmon—about 60 per cent for the

last eight years shown, as against 70 per cent for the latter species. A somewhat similar difference was obtained in the tagging experiments involving the two species (p. 460). Total chum tag returns from the commercial fishery were only 16 per cent as compared with about 30 per cent for pinks. The conclusion seems quite justified that the total chum populations are generally somewhat less heavily fished than the pink salmon stocks. This conclusion is in general agreement with results obtained from fish tagged in Johnstone Strait in 1945, although quite probably both species are somewhat more heavily exploited in these southern areas than in the central region (cf. DeLacy and Neave, 1947; Chatwin, MS). Average exploitation in the central region, by reasoning along lines indicated on page 461, should approximate 40 to 50 per cent.

A lower rate of exploitation of chums would be expected since fishing is usually closed before the later chum runs have passed through the fishing areas, whereas the more compact pink salmon migration is well covered by the fishing season (although temporary closures of the fishery are applied in accordance with estimated conservational requirements).

TABLE XI. Reported catch and escapement of chum salmon in the central region of British Columbia.

Year	Catch	Escapement	Total run	Percentage caught
1934	589,560	558,375	1,147,935	51
1935	1,029,640	957,200	1,986,840	52
1936	668,040	1,515,850	2,183,890	31
1937	899,450	828,725	1,728,175	52
1938	993,850	962,950	1,956,800	51
1939	598,990	414,775	1,013,765	59
1940	568,090	640,875	1,208,965	47
1941	836,700	962,975	1,799,675	47
1942	591,370	544,800	1,136,170	52
1943	833,600	654,250	1,487,850	56
1944	587,010	464,650	1,051,660	56
1945	1,035,460	1,092,225	2,127,685	49
1946	1,801,410	874,450	2,675,860	67
1947	2,243,010	1,178,200	3,421,210	66
1948	1,809,160	385,250	2,194,410	82
1949	1,098,590	705,080	1,803,670	56

CHANGES IN ABUNDANCE OF ADULT CHUM SALMON

Examples of annual changes in chum salmon runs, catches or escapements are presented in Figures 6 to 8 (see also Hoar, 1951).

The fluctuations shown by these graphs are of considerable amplitude and irregular frequency. There is no tendency for regular recurrence of large or small runs; nor is there evidence of sudden change to persistent new levels of higher or lower abundance. These features are no doubt associated with the varying life-span, which to some extent distributes over two or more years the effects of mortality changes taking place in a single season. Nevertheless, pronounced peaks and depressions occur. These do not synchronize with the length of the life-cycle,

whether this be taken as four years (which is usually true for a large majority of the individual fish) or whether some allowance be made for a percentage of fish of other ages. Evidently abundance is commonly determined by factors other than the size of the escapement.

The Mechanism Controlling Population Levels

As is the case with pink salmon, the mortality attending the life-cycle of the chum may be compensatory, depensatory or extrapensatory in its effect.

Compensatory mortality is again attested by the fact that the species is still commercially plentiful after many years of fishing which, even if somewhat less severe than that which has been applied to pink salmon, can yet be described as intensive.

It must again be supposed that this type of mortality is characteristic of the period between the entrance of the adults into fresh water and the emergence of the fry, that is, the period in which density is at a maximum due to environmental limitations. Owing, however, to the variable physical conditions in the chum salmon streams hitherto examined, a good inverse relationship between population size and reproductive efficiency cannot be demonstrated by a short sequence of annual records. It would presumably become apparent as a long-term average but in any given year compensatory effects are likely to be outweighed by extrapensatory factors. In view of the character of the streams commonly utilized by chums, this is likely to be generally true for the species.

The effects of predation on migrating fry have been investigated at Nile Creek and Hooknose Creek by the liberation of marked fry at a distance above the counting weir at intervals during the period of fry migration. At Nile Creek experiments were conducted by the writer in 1946 and 1947 and in subsequent years by Mr. W. P. Wickett. A similar experiment was performed in 1951 at Hooknose Creek by Mr. J. G. Hunter, at the writer's request.

The general features of predation during this phase of the life-history of the chum salmon are in conformity with the data obtained by Cameron (1941) for pink salmon at McClinton Creek. Conclusions may be summarized as follows:

1. Percentage mortality *increases* with the distance over which the fry travel.
2. Percentage mortality *decreases* with increasing number of migrants.
3. Percentage mortality *increases* during the progress of the run.

Points (2) and (3), which are of chief interest for the present discussion, are illustrated by Table XII which presents Hunter's data for Hooknose Creek. Thread-marked chum fry were released weekly in lots of about 100 at a distance of 300 yards upstream from the counting weir. Recoveries were made at the weir, where the total number of migrants was also counted. While unfortunately a test was not feasible during the peak week of the migration, the results indicate clearly that percentage survival increased as the total number of migrants became greater and declined as the run fell off during the later weeks. Also, percentage survival was less during the declining phase of the run than at corresponding population levels prior to the peak.

The end result therefore appears to depend on (*a*) the *size* of the fry population, (*b*) the *timing* of the migration, (*c*) the *compactness* of the migration. Factor (*a*) involves a *depensatory* relationship. Variations in (*b*) and (*c*) will be *extrapensatory* in effect and may therefore either reinforce or reduce the effects due to (*a*). For example, the advantage possessed by a large population would presumably be reduced if its exodus were spread over a long period so that the numbers migrating at any one time were relatively small. A late migration would also be at a disadvantage unless a similar lag occurred in the presence or activity of predators.

In comparing the fry runs of different years, the following estimates have been made for chum salmon at Nile Creek (Table XIII).

TABLE XII. Survival of marked chum fry in relation to total numbers of pink and chum fry migrating at Hooknose Creek, 1951.

Week ending	Number of fry migrants reaching weir	Estimated number of fry emerging	Percentage survival of marked chums
April 7	4,976	11,309	44
14	20,188	34,216	59
21	46,741	69,762	67
28	224,696	....	....
May 5	218,970	391,017	56
12	95,921	213,157	45
19	48,178	160,593	30
26	3,271	21,806	15
June 2	1,539	6,412	24

TABLE XIII. Number of fry migrants and percentage survival of marked chum fry at Nile Creek.

Year	Number of fry migrants reaching weir	Estimated number of fry emerging	Percentage survival of marked chums
1946	138,388	223,000	62
1947	8,319	18,500	45
1948	4,808	8,600	56
1949	23,188	66,800	35
1950	782	2,170	36

The size of the runs at Nile Creek during these years has been so small that little range is presented for exhibiting depensatory effects at varying levels of abundance. However, the one "large" run which produced 138,000 survivors was accompanied by an estimated loss of 38 per cent, whereas the four runs which yielded survivals of from 800 to 23,000 individuals showed an average mortality rate of about 57 per cent. Actually the discrepancy was probably greater, since the 1946 tests were made over a longer distance of travel which presumably involved increased mortality.

It is concluded that depensation is a factor of real significance in determining the adult abundance of this species, the very considerable effects of fry losses working generally to the detriment of populations which have become small through other causes.

Whereas compensatory mortality tends to maintain a uniform abundance from year to year and depensatory mortality tends to increase and perpetuate such deviations as can still arise, the considerable and irregular fluctuations which in fact occur point to the variability of mortality which cannot be referred to either of these categories. It has already been suggested that the freshwater habitats of chum salmon are particularly susceptible to variation in physical conditions and these are regarded as providing a major source of the fluctuations observed. Other extrapensatory variations are no doubt imposed in the ocean.

The same general processes determine population levels in both pink and chum salmon. The features which distinguish the pattern of variation of the latter species are associated with the relatively greater part played by extrapensatory mortality and the greater flexibility of the life-span.

Relative Effects of Freshwater, Natural Ocean and Fishing Mortality in Determining Population Levels

As already indicated, the average marine mortality of chum salmon is considered to be at most only slightly different from that of pink salmon and there seems to be no reason for supposing that it is more variable. The situation is otherwise, however, with regard to freshwater losses. The combined results of Nile Creek and Hooknose Creek show an efficiency of fry-migrant production ranging from 15 to 0.08 per cent, or a ratio of 187:1. Such extreme variation of course cannot be expected to apply to the populations of large areas containing numerous spawning streams but, taken in conjunction with the opinion expressed previously that marine mortality is largely non-compensatory, it gives good grounds for supposing that freshwater conditions play the major part in determining changes in the abundance of adult populations. This conclusion is supported by the correlation established by Wickett (Neave and Wickett, 1949) between seasonal stream flow and the abundance of adult chums four years later, in the Vancouver Island district.

The effect on the spawning stock of varying rates of freshwater survival and fishing intensity are shown in Figure 9. In these graphs a figure of 4 per cent has been assumed to represent average natural ocean survival. Average egg-production per pair of fish is taken as 2,700.

On the basis of these assumptions the average freshwater survival in the absence of any fishery should be less than 2 per cent. To maintain a constant level with a 50 per cent fishing mortality, which has been suggested as an approximate average, freshwater survival should be 3.7 per cent. It can be seen from Table IX that in the combined Nile Creek and Hooknose Creek records this level has been definitely exceeded in four instances, definitely not attained in four other instances and approximately equalled in the remaining instance.

Conservation Problems

Trends in the chum salmon stocks of large areas are difficult to assess because (*a*) the collection of accurate statistics has been impeded by the varied manner in which this species is commercially processed and sold (Hoar, 1951), and (*b*) the large and irregular fluctuations prevent the drawing of sound conclusions from data which do not extend over a long period of years.

The data available for the central region (Figure 7) do not show a pronounced upward or downward trend. However a decline, at least in the size of *escapements*, is certainly suggested by the graph for the Vancouver Island region (Figure 8). A decline in escapement, caused by increasing fishing intensity, might of course be made good by increased reproductive efficiency. The downward trend in this instance, however, seems to have continued over a long period and there must come a point at which compensation cannot close the gap. This is an area of relatively intensive fishing but if Nile Creek results are indicative, some of the streams are in fact yielding a very low output in many years, instead of responding to the reduced density of the spawning populations. As far as this stream is concerned, the fry output in three out of five observed seasons would, by any reasonable calculation, produce a smaller returning population even if no fishery were operating. While Nile Creek probably represents an extreme case, concern may well be felt regarding the productivity of other streams in this region at the present time. A chronic condition of low reproductive efficiency caused by the physical condition of the spawning streams cannot be cured by regulation of the fishery.

The fact that relatively small spawning escapements may produce large returning populations, and vice versa, may suggest that the size of adult runs, within existing limits, is independent of the size of escapements and that a more intensive fishery could be prosecuted without harming the stocks. It may be strongly urged, however, that the observed fluctuations are in large measure caused by mortality which is non-compensatory. Observed instances of large spawning populations producing small returns do not permit the establishment of a generalization regarding the inefficiency of large escapements. The probability must be envisaged that a smaller population would have produced an even smaller return *in the particular years concerned.* Runs could, of course, be utilized more economically if it were possible to foresee the particular climatic conditions to which their eggs and alevins will be exposed. The minimum size of escapement required to produce a given output of sea-going fry would vary greatly from year to year. The existence of an underlying compensatory process cannot be doubted, but the extrapensatory variations which are imposed upon it are so large that "slumps" and "booms" frequently occur. The difference between pink and chum salmon in this respect is of course in degree only and is considered to be largely a reflection of an average difference in freshwater habitat. Under similar conditions, as shown by the results at Hooknose Creek, populations of the two species react in a similar manner.

Speaking broadly, pronounced instability of physical conditions in spawning

streams is viewed as tending to eliminate pink salmon, by reason of the low egg-production and rigid life-span. With chum salmon it induces great variation in population size. Maintenance of favourable conditions during incubation and alevinage would tend both to increase the average output and to reduce fluctuations. If this were achieved by controlling the flow of spawning streams (or portions of them), it could be expected that compensatory effects would become apparent—that is, a stricter relationship between the size of the escapement and the efficiency of individual reproduction would be observed. The intriguing possibility that increased stability might tend to enable pink salmon to displace chums is also presented.

The general effects of predation have been shown to be similar with respect to the fry migrants of both species, in that small populations will tend to suffer relatively heavier losses than large populations. Elimination of, or protection from, predators should therefore be a major consideration in establishing new runs or in building up stocks which have reached a low level of abundance.

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